

REVIEW OF THE DERODONTIDAE (COLEOPTERA:
POLYPHAGA) WITH NEW SPECIES FROM
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ABSTRACT

The world genera and species of Derodontidae are reviewed, and keys are provided to genera (based on larvae and adults), to the species of *Nothoderodontus*, and to the North American species of *Derodontus* and *Laricobius*. Discussions are presented on the adult and larval morphology, habitat and food habits, life cycle patterns and phylogenetic relationships of the family. A family diagnosis is presented and two possible generic cladograms are proposed. A special section is included on the surface features associated with cuticular secretions in beetles as a whole, as well as in derodontids. The following new taxa are described: *Derodontus esotericus* Lawrence, *D. unidentatus* Lawrence, *Nothoderodontus chilensis* Lawrence, and *N. dentatus* Lawrence.

INTRODUCTION

The family Derodontidae includes four genera and 19 species of small-sized beetles which inhabit the temperate parts of both southern and northern hemispheres but are rarely encountered in the field and uncommon in collections. Although treated as clavicorn Cucujoidea in older classifications, they are considered by Crowson (1944, 1955, 1959) to be among the most primitive of polyphagan beetles, and Hlavac's work on the prothorax (1973, 1975b) has given support to this idea. In the present work, a systematic review of the Derodontidae, with descriptions of new taxa from North America and Chile, is combined with a detailed presentation of adult and larval external morphology, accumulated data on food habits and life cycle, and a discussion of phylogenetic relationships within the family and between it and related groups of beetles.

ADULT MORPHOLOGY

A detailed morphological study of *Laricobius erichsoni* has been published by Franz (1958), and specific structures of various derodontids have been illustrated by Brown (1944), Crowson (1944, 1955, 1959), Forbes (1926), Hlavac (1973, 1975b), and Stickney (1923). The following sections will emphasize those features unique to the family, those primitive for the order as a whole, and those which are of use in determining intrafamilial relationships. Because an emphasis has been placed on spatial and functional relationships, some of the terminology (taken in part from Hlavac, 1973, 1975b) will be at variance with that normally employed in taxonomic keys. When possible, alternative terms are given in parentheses. A separate section dealing with surface features in Coleoptera has been included because the general subject has not been adequately covered in the literature.

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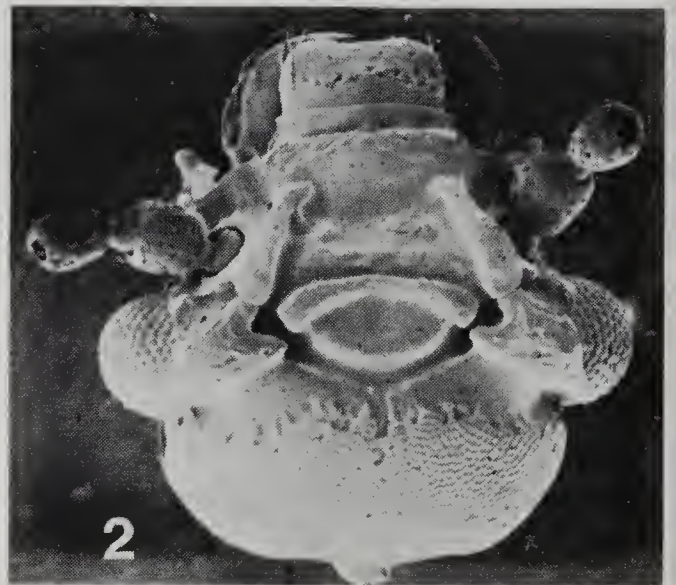
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Structural Organization

Derodontidae are small, relatively loosely organized beetles, which are highly convex dorsally and flat ventrally. The vestiture in *Peltastica* and *Derodontus* consists of very short, fine hairs, whereas in *Laricobius* the hairs are long and erect, and in *Nothoderodontus* they are long and recumbent.

Head and Mouthparts. The most conspicuous feature of the derodontid head is the pair of dorsal ocelli (figs. 1-4, 7) just mesad of the compound eyes. The function of these organs is unknown and it is not at all certain that they are homologues of the ocelli of Hydraenidae and omaline Staphylinidae; their location immediately over the optic nerves and the thin, translucent cuticle of which they are composed, however, suggest that they are at least analogous to the dorsal ocelli of other beetles. In *Peltastica*, *Laricobius*, and *Nothoderodontus* they are relatively small, round, and close to the eye margins, while in *Derodontus* they are much larger and are incorporated into the system of canals and bridges described in the next section (p. 379).

The compound eye is relatively large, entire, and finely faceted; in *Laricobius* and *Nothoderodontus*, setae occur among the eye facets. The an-



Figs. 1-4. Heads of adult Derodontidae, dorsal view. 1. *Derodontus esotericus*, n. sp. 2. *Derodontus unidentatus*, n. sp. 3. *Nothoderodontus chilensis*, n. sp. 4. *Nothoderodontus gourlayi* Crowson.

tennal insertions in *Peltastica* are concealed from above by antennal ridges formed from the frons; these ridges are reduced in the remaining three genera, so that the antennal insertions are exposed. *Peltastica* also has well-developed antennal fossae beneath the eyes, but the other genera lack them. In all derodontids, the cervical sclerites are well-developed, the frontoclypeal suture is absent, and the tentorium consists of a well-developed corporotentorium, broad laminatentoria meeting at the midline, strong pretentoria and relatively short supratentoria. Antennae in all genera are 11-segmented, with a weak, 3-segmented club, each club segment bearing a few simple sensillae at the apex. That portion of the head capsule which is enclosed by the anterior edge of the pronotum has a surface structure consisting of plates, which on the lateral surfaces may be slightly overlapping.

The mouthparts in all derodontids are more or less enclosed by the large labrum, mentum, and stipites fitting together against the flattened mandibular apices (figs. 5-6, 8). In *Peltastica*, the mandible has a well-developed, fringed prosthema and extensive, tuberculate mola, the galea has a well-developed apical brush, the lacinia bears 2 apical spines, and the labial glossae are broad. In *Nothoderodontus*, the mouthparts are similar, except for a slight reduction of the galeal brush. In *Derodontus*, the mola, galeal brush, and labial glossae are further reduced, while in *Laricobius* all of these structures are extremely reduced, and the lacinia bears a single apical spine. These differences appear to be correlated with feeding habits, which are essentially similar to those of the larvae (see p. 384).

Prothorax and Pleurocoxal Mechanism. The prothorax is relatively small and at least slightly expanded laterally, with a low notal volume and a membranous notosternal joint. A remnant of the anterior pleural flange is distinct in *Peltastica* and *Laricobius*, but reduced in *Derodontus* and *Nothoderodontus*. The pleuron is rigid, so that the possibility of coxal flexation is lost; a similar result is achieved, however, by the bending of the coxal apex, so that rotation produces antero-posterior movements. The trochantin and coxal articular region are exposed in *Peltastica*, *Laricobius*, and *Derodontus*, but in *Nothoderodontus* they are completely concealed by the notal cowling. The coxal cavities are internally open and externally open (*Laricobius*) or closed (other genera). The notal projections (postcoxal processes) are broad and enclose the plated surfaces of the mesepisterna. In *Laricobius*, they do not form a complete collar, so that the cavities are open behind and the coxae are housed partly by mesosternal concavities. In *Peltastica*, the notal projections meet at the midline behind the sternal projection (intercoxal process), closing the coxal cavities and forming a complete posterior collar. A complete collar is also formed in *Derodontus* and *Nothoderodontus*, but the notal projections fit into depressions in the apex of the sternal projection. The notal processes are molded in such a way as to allow free travel of the coxal apices. The sternal projection is relatively flat and does not extend ventrally between the coxal apices; the apical portion is not or only slightly expanded in *Peltastica* and *Laricobius*, but in both *Derodontus* and *Nothoderodontus* it is strongly expanded on each side where it meets the notal projections.

Pterothorax and Legs. The pterothorax is loosely organized, with both sternopleural suture and meso-metasternal attachment membranous. The median projections (intercoxal processes) of the sterna are relatively narrow; in *Peltastica* and *Laricobius* they do not or only barely meet, so that

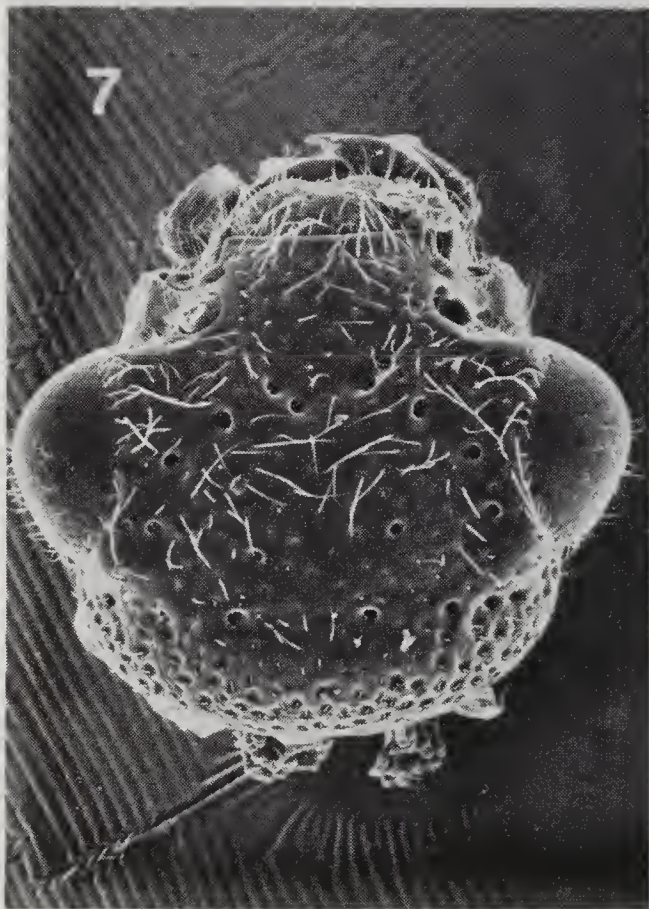


Fig. 5. Head of adult *Nothoderodontus gourlayi* Crowson, anterolateral view. Figs. 6-7. Head of adult *Laricobius rubidus* LeConte. 6. Lateral view. 7. Dorsal view. Fig. 8. Adult *Derodontus maculatus* (Melsheimer), ventrolateral view.

the mesocoxae are almost contiguous, but in *Derodontus* (fig. 8) and *Nothoderodontus* the mesosternal process slightly overlaps that of the metasternum. The mesotrochantin and mesocoxal articular region are exposed in all genera. In derodontids, both the mesepimeron and metepisternum

form part of the perimeter of the mesocoxal cavity, a condition unique within the Polyphaga but occurring in both Myxophaga and Archostemata. The middle coxae have bent apices like the procoxae and the relatively low coxal cowlings allow free movement. The anterior part of the mesepisternum consists of a plated surface (fig. 15), which is concealed by the prothorax, while other portions of the pleuron and sternum have pits and channels described in the next section.

The metathorax is long relative to the mesothorax and abdomen, with a long median suture (metendosternal invagination) and at least a partial posterior transverse suture on the sternum. The median suture in *Nothoderodontus* extends about half the distance between meso- and metacoxae, whereas in the other three genera, it extends almost the entire length of the sternum. The transverse suture is almost complete in *Peltastica*, broken on either side of the midline in *Laricobius*, and distinct only at the midline in *Derodontus* and *Nothoderodontus*. In all derodontids, the outer edge of the metepisternum is produced laterally near the anterior end to form an interlocking device with the edge of the elytron. In *Peltastica* and *Laricobius*, it is only weakly developed, but in *Derodontus* (fig. 8) and *Nothoderodontus* (fig. 16) it is distinct and posteriorly curved. In *Peltastica*, the interlocking process fits under the elytron, which is not modified for its reception. In the other genera, the process locks on the outside of the elytron, so that its apex is visible (fig. 8); the elytron at this point is notched for its reception. Surface features of the metathorax are described in the next section.

The metendosternites of *Laricobius* and *Derodontus* have been illustrated by Crowson (1944) and are of a unique type, with a short, broad stalk and narrow lateral arms strongly expanded at the apex. Those of *Peltastica* and *Nothoderodontus* resemble the *Derodontus* type in having the median process divided into 2 rounded lobes and the lateral arms longer and strongly curved.

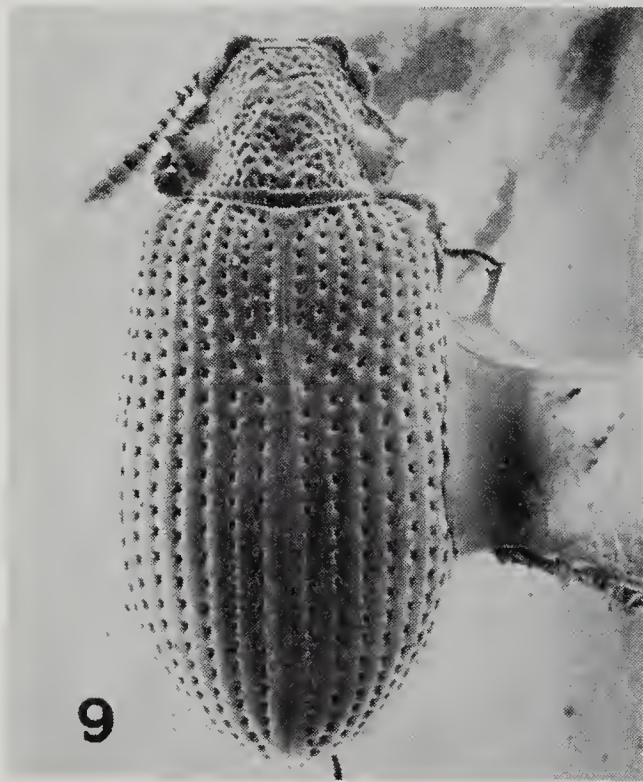
The metacoxae are somewhat motile, have a transverse anterior edge, and extend from near the midline to the rim of the elytra. The posterior face of the coxa is vertical and somewhat excavate, isolating the planes of the metasternum and abdomen and blocking forward movement of the hind leg. The coxa is somewhat triangular in outline, with the median edge extending further posteriorly than the lateral one; the posterior extension is most pronounced in *Peltastica* and *Derodontus*, much less so in *Laricobius* and *Nothoderodontus*.

The legs are relatively short, and the hind femur never extends far beyond the lateral edge of the coxa. In *Peltastica*, *Derodontus*, and *Nothoderodontus*, the tibial apex is simple, with 2 spurs at the inner apical angle, the first three tarsal segments are more or less equal, the fourth is slightly reduced, and the fifth is as long as (*Derodontus*, *Nothoderodontus*) or longer than (*Peltastica*) the first four taken together. In *Laricobius*, the tibiae are slightly expanded subapically, with a setal comb at the apex, the tibial spurs are absent (or at least not distinguishable from the comb setae), and the first three tarsal segments are enlarged and lobed beneath.

Elytra and Hindwings. The elytra of *Peltastica* each bear a scutellary striole and about 20 irregular rows of round punctures, the latter being of the windowed type with very thin cuticle comprising the floor of each. The epipleura are explanate with a serrulate edge. In *Laricobius*, the scutellary

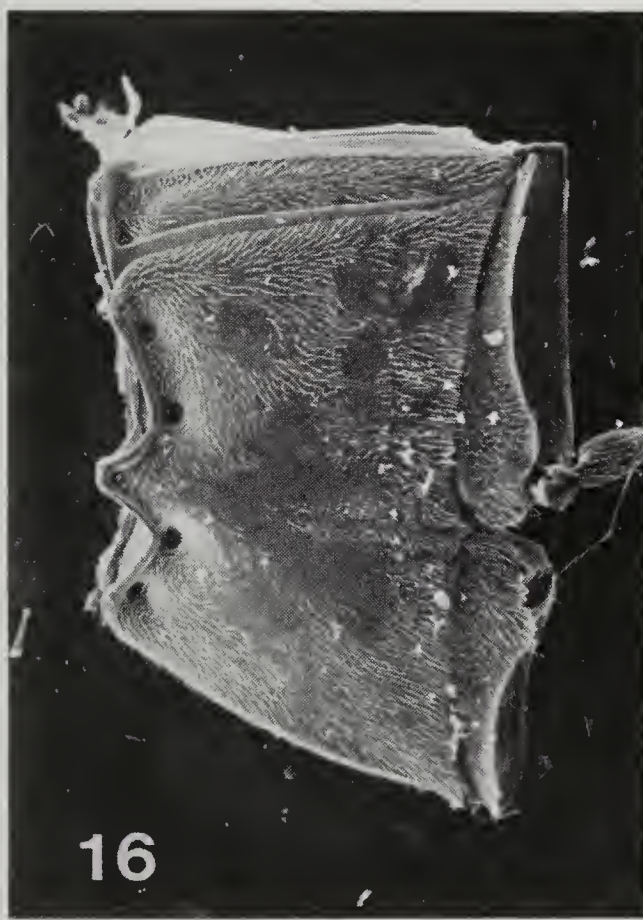
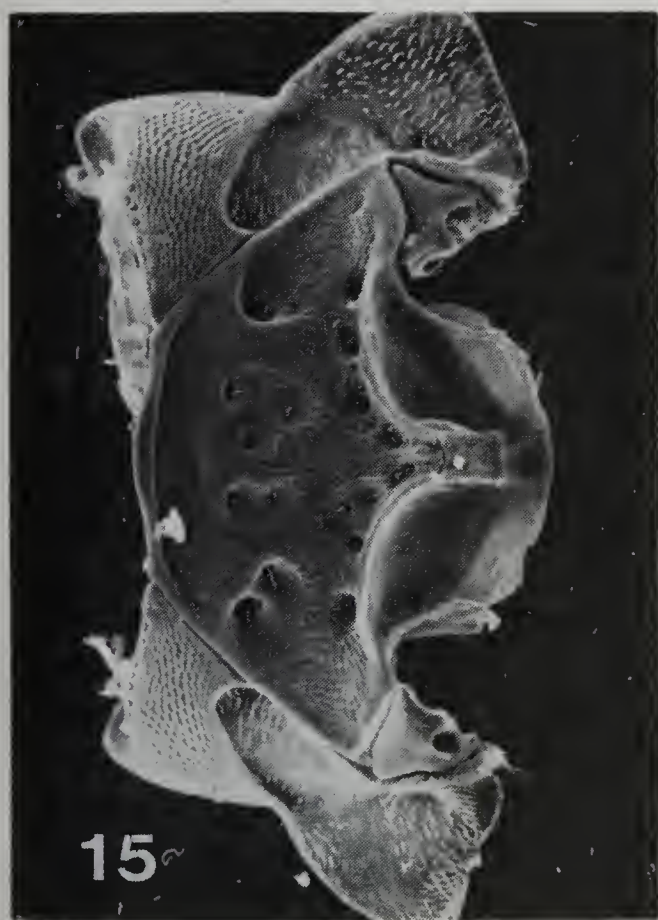
striole is present and each elytron bears 10 rows of round, windowed punctures. The scutellary striole is also present in *Derodontus*, but each elytron bears 11 rows of punctures, each of which may be somewhat quadrate in shape and pinched in the middle by minute lateral projections (figs. 9-12). In *Nothoderodontus* (figs. 13-14) there are no scutellary striae, and each elytron bears 11 narrow, deep striae, within which minute punctures are unevenly distributed; in addition there are deep pits at the bases of striae 9, 10, and 11. The lateral elytral edges in *Derodontus* are serrulate, as in *Pelastica*, whereas those of *Laricobius* and *Nothoderodontus* are smooth.

The derodontid hindwing is characterized by having a relatively long



Figs. 9-12. Adult *Derodontus* spp., dorsal view. 9. *D. esotericus*, n. sp. 10. *D. maculatus* (Melsheimer). 11. *D. trisignatus* (Mannerheim). 12. *D. unidentatus*, n. sp.

membrane, which must undergo considerable transverse folding to fit beneath the shortened elytral space, and a distinctive break in the costa at the position of the major transverse fold. In *Peltastica*, there is a weakly developed radial cell, short, oblique radial sector (called a spur off r-m by Crowson, 1955: fig. 81), a distinct r-m crossvein slightly broken in the middle, a moderately long median vein basad of the cu-m junction, an api-



Figs. 13-14. Adult *Nothoderodontus* spp., dorsal view. 13. *N. gourlayi* Crowson. 14. *N. chilensis*, n. sp. Figs. 15-16. Thorax of adult *Nothoderodontus chilensis*, n. sp. 15. Mesothorax, ventral view. 16. Metathorax, ventral view with right pleuron removed.

cal extension of the median vein which reaches the edge of the membrane, a well-developed cubitus extending almost to the edge of the wing, a distinct W cell, 5 anal veins, and a jugal lobe which contains a single vein. Reduction occurs in the wings of the other three genera, so that the radial cell and radial sector are vague or absent, the r-m crossvein more interrupted, the median vein shorter basally (especially in *Derodontus*), the apical part of the cubitus and apical extension of the media lost in *Nothoderodontus*, the anal veins reduced to 4 in *Derodontus* and *Nothoderodontus*, and 3 in *Laricobius*, the W cell lost in *Nothoderodontus*, and the jugal vein lost in all three.

Abdomen and Genitalia. The abdomen in derodontids has five well-sclerotized visible sternites (ventrites) belonging to segments III through VII. In addition, the strip of cuticle just above the hind coxae and in front of the third sternite probably represents a remnant of Sternite II, as pointed out by Crowson (1959). The anterior projection of the third sternite is slender and extends between the nearly contiguous coxae, but it does not come into contact with the metasternum. The five visible sternites are free, except in *Laricobius*, where the first two (III and IV) are fused. The 8th, 9th, and 10th segments are invaginated and not as heavily sclerotized as the more basal ones. Well-developed episternites occur on III through VII and bear broad interlocking patches, which decrease sharply in height posteriorly. Sclerotized, undivided tergites occur on segments II through VIII and each of these segments bears a functional spiracle on each side. Sternite III in *Derodontus*, *Laricobius*, and *Nothoderodontus* bears two parallel, longitudinal ridges near the midline (fig. 8). In *Laricobius*, there is an additional median ridge on IV and a reduced median tubercle on V, while in *Derodontus*, these median structures extend to sternite VI. In addition, there may be lateral impressions or deep pockets on the sternites, which are discussed under surface organization.

The eighth sternite has a more or less well-developed median anterior strut. The 9th sternite in all male derodontids forms a ring-like structure (fig. 24) with an ovoid apical sclerite attached to basal struts which meet anteriorly. Laterally, this sternite is attached to a single tergite (*Nothoderodontus gourlayi* fig. 31) or more commonly two hemitergites (called pleurites by Crowson, 1955), which meet at a narrow junction point (*Laricobius* and *Peltastica*) or fuse along a broader area (*Derodontus*, fig. 24; Chilean *Nothoderodontus*). Beyond this, forming the apex of the abdomen, is the 10th tergite, which is referred to by Crowson (1955) as tergite 9. The homologies of these apical sclerites are still in dispute, but we can see no good reason why this terminal segment, which is closely associated with the anal opening, should not be a remnant of segment 10. This type of abdominal apex appears to be primitive in the Polyphaga and occurs in basal staphylinoids, such as *Necrophilus*, in *Eucinetus*, and in various Elateriformia. In *Necrophilus* and *Eucinetus*, there is an undivided 9th tergite, suggesting that the condition in *Peltastica* and *Laricobius*, although presumably primitive for the family, may be a derived feature within the Polyphaga.

In the female, the 8th sternite lacks a median anterior process, while the hemitergites of segment 9 do not meet dorsally. The ovipositor is short, with valvifers (sternite 9), one-segmented coxites, and styli which may be short and lightly sclerotized (*Laricobius*) or longer and more heavily-sclerotized (*Derodontus*).

The aedeagus (figs. 27-30, 32-37) consists of a well-developed, ventrally sclerotized basal piece, two parameres, and a median lobe, which is partly enclosed by the bases of the parameres both dorsally and ventrally. In *Peltastica*, the basal piece is fairly large, the parameres long and deeply notched at the apex, and the median lobe long and tubular, with short basal struts and a terminal opening surrounded by fine strengthening ridges. In *Laricobius*, the basal piece is smaller, the parameres may be notched or simple at the apex, and the median lobe is somewhat broader with a subacute apex. In *Derodontus*, the basal piece is usually large and quadrate, the parameres are distinctly notched at the apex and the median lobe bears a ventral carina along the midline and varies considerably in apical configuration, position of the opening, and length of basal struts (figs. 34-37). In *Nothoderodontus* the carina is absent on the median lobe. The parameres in the Chilean species are simple and narrowly rounded or subacute at the apex (fig. 32), while those of *N. gourlayi* are broadly notched at the apex (fig. 29). The median lobe in the Chilean forms has a pair of basal struts (fig. 33), while in *N. gourlayi* there is a single median strut (fig. 30).

Surface Organization

Derodontids exhibit complex variation of systematic importance in surface molding, and it appears that these surface features may be the cuticular components of a chemical defense system. A preliminary context for their interpretation in beetles as a whole is developed here, before considering variation and functional role within the family itself.

Although cuticular secretions have diverse functions, including protection from water loss, sexual attraction, and appeasement of ant hosts (see below), a defense emphasis seems likely in the forms discussed here. As cogently argued by Duffey (1977), chemical defense can offer protection against macropredation, micropredation (bacteria and fungi) or both. Broad spectrum defense is probably most common in hydric forms where both sorts of enemies are abundant and diverse.

In some substrate dwelling beetles, much of the body becomes covered with an opaque crust, which may be entirely secreted or represent an amalgam of epicuticular wax and detritus. The function of encrustation in these forms has not been demonstrated, but defense, broadly defined, is a reasonable assumption. Defense through concealment must also be considered for those few encrusting beetles that live on surfaces. In other cases, material may be secreted without noticeable build-up, either because volatile elements have evaporated or because thin layers of transparent waxes are not easily perceived. Whatever the chemical and functional diversity of exocrine products, the cuticular components of specialized systems conform to a few basic types, broadly distributed within the Coleoptera.

Encrustation may occur without obvious surface structures other than setae and scales, as in *Aesalus* (Lucanidae), *Microchaetes* (Byrrhidae), and certain *Cis* (Ciidae). More often secreted, encrusted material is stored, contained, and distributed by linear or circular invaginations or evaginations. Simple elements, such as deep pores, shallow basins, elongate channels, conical and cylindrical projections, linear ridges, often with countersunk canals, and bievaginational bridges may be combined to produce some of

the most elaborate surface configurations within the Insecta. An incomplete distribution of each category or modification is given below. An asterisk after a generic name indicates that the structure mentioned is consistently encrusted; a double asterisk indicates a densely setose surface.

Conical invaginations, at least several times as long as the cuticle is thick, occur without associated channels in only a few groups, such as *Tmesiphorus*** (Pselaphidae). Typically, deep pores open onto much shallower canals or grooves, which may also secrete or merely transport material across body surfaces. Pores with associated canals are present on the prothorax of *Anthicus*** (Anthicidae), *Lycoperdina* (Endomychidae), *Enicmus** (Lathridiidae), and *Dasycerus** (Dasyceridae), while in *Tmesiphorus*** and in other pselaphids they occur on the mesosternum and abdomen as well. Containment and storage may be within shallow basins, such as on the head of *Enicmus**, where large pores are absent, or in the same animal in the mesal portions of the meso- and metasternum where several pores are clustered.

Channels without associated pores are to be found on the head and or pronotum in *Cupes*** (Cupedidae), *Helophorus** (Hydrophilidae), *Ochthebius* (Hydraenidae), *Georyssus** (Georyssidae), *Tmesiphorus***, *Dasycerus**, *Syncalypta** (Byrrhidae), *Sarothrias** (Jacobsoniidae), most Passandrini* (Cucujidae) and all Rhysodidae*. In many of these forms, longitudinal channels occur on the elytra as well. Along a short portion of their route, channels may be partly or wholly covered by paired evaginations forming "natural bridges". The canal below and between the evaginational bridge elements is often countersunk, i.e. lower than surrounding channels. These curiosities may serve to increase even further the surface available for secretion and storage and for binding materials to body surfaces. At least partial bridges are found on the head in *Salcedia** (Carabidae) and *Clinidium** (Rhysodidae); on the prothorax of *Axiocerylon** (Cerylonidae), *Colydodes** (Colydiidae), and *Archaeoglenes** (Tenebrionidae) (Doyen and Lawrence, 1979); and on the abdomen of *Micropeplus** (Micropeplidae) and *Georyssus**.

The trichomes of certain myrmecophilous and termitophilous beetles represent elaborations of this type of structure, where the inner surfaces of evaginations are densely setose, thus increasing the volume of fluid stored by capillary action, reducing the rate of evaporation, and facilitating ingestion by the ant host species. Complete bievaginational bridges occur on the prothorax of *Edaphopaussus*** (Carabidae), and *Gnostus*** (Ptinidae) and on the elytra of the Rhyparini** (Scarabaeidae). The prothoracic trichomes in *Cremastochilus*** (Scarabaeidae) and *Thorictus*** (Thorictidae) are developed from single evaginations but bear dense setae on contiguous unevaginated surfaces.

A series of ridges set between low lying areas may serve the function of containing encrusted matter and protecting it from abrasion; these occur in *Salcedia**. A network of low lying ridges may serve the same function on the prothorax of *Micropeplus**. Discontinuous enclosures are formed from large numbers of small to large tubercles on the head and prothorax of *Omma** and *Tetraphalerus** (Cupedidae), and on the elytra of many beetles, including *Lepicerus** (Lepiceridae), *Spercheus** (Hydrophilidae), *Tympanogaster** (Hydraenidae), *Dasycerus**, *Georyssus**, Trogidae*, *Hendecatomus** (Bostrichidae), *Calitys** (Trogositidae), *Priastichus** (Phloeostichidae),

many Colidiidae*, *Cotulades** (Zopheridae), and the tribe Bolitophagini* (Tenebrionidae).

These various instances of topographic irregularity form a family of adaptations for controlling the flow and storage of materials on cuticular surfaces. A language based on hydrology seems appropriate for their discussion, so that the surface of a given beetle can be perceived as consisting of a number of drainage and containment systems.

Many of the adaptations discussed above, including pits, pore-canals, channels, basins, and bievaginational bridges, are present in Derodontidae. Encrustation, however, is sporadic and rarely extensive or well-developed (see below). Individual structures are considered separately, followed by a discussion of patterns of divergence involving the entire system. Since we have not studied gland histology, we can only speculate on the sources of secreted material.

Head. In *Peltastica*, the dorsal surface of the head contains many moderately deep pits, a number of which open onto a shallow epicranial impression. There are fewer, somewhat larger invaginations in *Laricobius* that are dispersed among a large number of smaller setiferous punctures (fig. 7). Between the eye and antennal insertion is an ovoid, setose cavity (fig. 6) which gives rise to a trio of long, slender invaginations, two of which are directed posteriorly behind the eye, and the third mesally. Ventrally there are two pits on the mentum which are connected by a shallow groove.

In *Derodontus*, elevation of the ocelli and a set of lateral and transverse ridges enclose, in a fence-like manner, several low lying areas and channels, while allowing for communication among them (figs. 1-2). The anterofrontal plain is bounded laterally by two long, oblique, posteriorly diverging ridges, each of which is joined to an ocellus by a complete bievaginational bridge that covers the anterior end of a deep, countersunk ocellar canal. Posteriorly, the plain is bounded by a slightly curved, transverse ridge, behind which is a flattened boss; the ridge is incompletely joined to the ocelli by a second pair of bridges over the ocellar canals. Each canal begins at a small, flat, setose area just above the anterior portion of the eye, continues posteromesally beneath the two bridges and then mesally behind the boss to join the canal on the opposite side. Each is also joined anteriorly to the plain and posteriorly to a broader and shallower channel continuing ventrally behind the eye. Only a few short setae are present on the surface of the head.

Of the three species of *Nothoderodontus*, the simplest, and presumably the most primitive, condition occurs in *N. chilensis* (fig. 3). A six-sided channel, formed primarily by invaginations, circumscribes the frontal region. Posteriorly, a broader, transverse canal extends between paired, small complete bridges. A sharp bend leads to a deep, posterior, lateral canal, which terminates at an anterior, complete bridge. As the canal shifts to an anteromesal course, the outer walls fall away above the antennal insertion and the canal then enters a narrow, deep, transverse channel, which is not to be confused with the frontoclypeal suture. The condition in *N. dentatus* can be derived from that in *N. chilensis* largely through an elaboration of preexisting structures (deepening of canals, enlarging bridges, and building a higher vertical wall behind the posterior rim of the antennal insertion). Even further development of these tendencies, combined with alterations in head geometry, yields the unusually complex head of *N.*

gourlayi (figs. 4 and 5). Maintaining the enlarged anterior bridge at near the level of the antenna, and moving the posterior transverse canal anteriorly beyond the eye's forward margin, greatly reduces the length of the posterior lateral canal and, consequently, the distance between the bridges (comp. figs. 3 and 4). The large foramen, bounded mesally by the posterior bridge, appears to represent the entire extent of a once linear canal. The long, very cryptic, zone of attachment between anterior evaginations is located at the base of the rear wall of the forward element of the posterior bridge. The broad anterior bridge is developed mesoventrally, bringing the anterior foramen of the cavity it encloses close to the antennal insertion, where a third bridge is formed (fig. 5). An oblique, transcephalic tunnel is thus formed, which joins dorsal and lateral regions. From the anterolateral foramen arise two channels: a broad, shallow one which extends ventrally to encompass much of the circumference of the antennal insertion, and a more sharply margined one which extends up to the anterior transverse canal. A pair of broad, shallow depressions may extend from the posterior transverse canal to the enclosed punctate region of the head; these are poorly developed in *N. chilensis*, but distinct in *N. dentatus* and *N. gourlayi*. In all species fine setae are abundant on all surfaces.

In *Peltastica*, *Laricobius*, and *Nothoderodontus*, the posterodorsal and posterolateral regions of the head, which are normally covered by the prothorax, are developed into an anterior band of large, setiferous punctures, and a posterior band of small, anteriorly inclined plates (figs. 3-6). Punctures are fewest and microsculpture least developed in *Peltastica*. In *Derodontus* (figs. 1-2), the punctate band is absent and only the scale-like plates are present. Ventral enclosed areas are smooth and lack punctures (figs. 6 and 8).

Aside from the numerous deep pores themselves, specialized storage surfaces are absent from the frons and vertex in *Peltastica* and *Laricobius*. Storage and transport surfaces are developed along altogether different pathways in *Derodontus* and *Nothoderodontus*, yet neither bears deep pores and both have a pair of bivaginal bridges on each side. In *Derodontus*, the containment strategy is based on a fence-like perimeter of ridges that enclose broad, low lying areas of topographic irregularity. Evaginations from the ocellus participate in the formation of both bridges, a deep, anterior transverse canal is absent, posterior canals continue behind the eyes, setation is sparse, and there is no enclosed band of setiferous punctures. In *Nothoderodontus*, containment is based on elevated regions of shallow curvature and countersunk invaginations without sharp margins; together these form a continuous channel that circumscribes the frontal region. The ocelli do not form bridges, the anterior canal is present, postocular basins are absent and setation is abundant. The genal basin in *Laricobius* is unique, although an analogous structure is present in *Nothoderodontus gourlayi*.

Prothorax. In *Peltastica*, there is a large number of shallow densely packed pores, nearly uniform in diameter and continuing up to the unmargined lateral rim. The pronotal disc lacks depressions. In other genera, the lateral regions are smooth, nearly impunctate, with single, large, anterior and posterior pores which are least developed in *Derodontus* (figs. 9-12) and very large in *Nothoderodontus* (figs. 13-14). Though convex in *Laricobius*, the lateral region is slightly concave in other forms and bordered by a slightly carinate rim, reduced in *N. gourlayi*. The disc of *Nothoderodontus*

and *Derodontus* may be slightly depressed and the large posterior pores may be connected by a narrow groove near the posterior rim. In both *N. chilensis* and *N. dentatus*, there is an additional pore on the pronotal hypomeron, near the base of the postcoxal process (notal projection).

Pterothorax. Except in *Peltastica*, the metacoxae are invaginated to form a transverse channel (figs. 8 and 16), which in *Laricobius* is joined to a deep pore. In *Laricobius* and *Nothoderodontus*, a series of pores and associated channels and basins on the meso- and metasterna almost completely surround the perimeter of the middle coxal cavities (figs. 15-16). In *Laricobius*, the margin of the mesosternal concavity which receives the procoxa is folded into a deep groove, which gives rise to a pair of conical invaginations. In *Laricobius* and *Nothoderodontus* the exposed portion of the mesepisternum is depressed, forming a shallow basin which leads to a slender invagination. In addition, the mesepimeron of *Laricobius* is produced ventrally into a cowl which encloses the coxal apex and is, in turn, covered by the mesepisternum. Slightly above the coxal rim, an invagination opens onto an oblique channel, which may be an unusually developed pleural suture. In *Nothoderodontus*, a single pore on the anteromesal rim of the mesepisternum opens onto a broad, shallow channel that extends almost to the hind coxa. In *Laricobius*, the metepisternal canal is deep and narrow, gives rise to three pores, runs directly below the elytral rim, and does not extend as far posteriorly. In *Derodontus*, the deep pores, basins, and canals associated with the meso- and metathorax are entirely lacking; instead the ventral surfaces (including the prosternum) are densely covered with large, shallow punctures (fig. 8), which on the mesopleuron and metepisternum are confluent, so that shallow basins are formed. In all forms, the enclosed portions of the mesothorax are covered with densely packed plates, which are counterparts of those on the head.

Abdomen. In all genera, but least so in *Peltastica*, the rim of each ventrite is carinate and borders a shallow depression. In *Laricobius*, the anterior portions of ventrites 2-4 (segments 4-6) are narrowly and deeply invaginated for about half their lengths with a deep pore at each end of the invagination. The fifth ventrite has a similar invagination just behind the middle but also a third pore at the anterolateral angle. In all groups, ventrites are joined so that the posterior member is quite concave, forming a narrow channel between them, which in *Laricobius* is continuous with the lateral canals. The median ridges on ventrites 3, 4, and 5 in *Laricobius*, *Derodontus*, and *Nothoderodontus* may also be part of this containment system.

Elytra. Except in *Nothoderodontus*, the elytral punctures are large and deep with unpigmented, translucent bottoms. Spaces between punctures are not impressed in *Peltastica* or *Laricobius*, and only slightly so in *Derodontus*. Punctures are round or oval in *Peltastica* and *Laricobius*, but in most species of *Derodontus*, they are somewhat elongate and bear small lateral projections that extend over the lumen forming incomplete microbridges (figs. 9-12). Similar kinds of "window punctures" are found in a number of other beetle families, such as Cupedidae (*Cupes*, *Omma*), Homalisiidae (*Homaligus*), Cantharidae (*Oontelus*), Zopheridae (*Usechus*, *Usechimorpha*), and Colydiidae (*Lasconotus*, *Pristoderus*). Such elytra seem to be adapted for storage of materials within pores, rather than transport along the surface. The opposite is the case in *Nothoderodontus*, where the small,

narrow punctures are set in deep channels and are clustered in anterior and posterior regions. Three large, posteriorly-facing pores open onto the bases of Striae 9, 10, and 11, which may secrete material passed along the canals formed by these striae.

Encrustation. In *Peltastica*, a continuous, opaque crust may cover the entire upper surface of the head, prothorax, and elytra; the ventral surfaces are bare. Increase in the number of indistinct rows of elytral punctures to over 20 and their dense packing may have the effect of enlarging the number of secretory sites and decreasing the distances between them, with resultant formation of this surface crust. In other genera of derodontids, a whitish, opaque material may be present only on the morphologically specialized areas, such as pores, grooves, canals, or basins discussed above. This material is difficult to see at lower magnifications and in no way affects the gross appearance of the animal. With both site-specific and broad surface encrustation, the build up of material follows the same pattern: little or none on teneral individuals, with variable amounts on fully pigmented specimens. Most museum specimens of *Derodontus* which we have seen are callow, with little or no encrustation. In mature forms, however, almost every elytral puncture is nearly filled with white material. In some species, the mass is held in place by paired bridges, demonstrating that it has been secreted at the puncture site and is not external detritus. Prothoracic punctures may also be filled with this material, while on the head, the deep canal between the bridges may be densely packed with secretion and the frontal plane occasionally covered as well. The metasternal punctures are commonly encrusted, but the canals between abdominal ventrites are only rarely filled. Though fewer specimens of other genera are available for study, all specialized structures in at least some examples bear a white crust. In *Nothoderodontus*, the elytral encrustation is restricted to the pores at the bases of the three outer striae.

Discussion. As a presumably non-rapid discharge mechanism, the defense system of derodontids could work by constant production of volatile material, along with a more persistent crust. By surrounding itself with a repulsive zone, a derodontid could be protected from some macro-predators. Clearly, the dorsal complex of secretory elements suffices for this. The organization of specialized ventral components suggests an additional role of protecting specific vulnerable regions leading to membrane and the elytral cavity. Site protection may be directed primarily at micro-predators, such as bacteria, fungi, or mites. For example, in *Laricobius* the following areas are bounded by pores, canals and basins: ventral surface of the head, lateral and ventral region of the pro-mesothoracic joint, meso-coxal perimeter, elytral rim adjoining most of the metathorax and nearly all of the abdomen, joints between abdominal ventrites. Though *Laricobius* is the most highly specialized in these respects, it may only have developed a morphological component increasing storage capacity of a chemical system functioning without such in other genera. Of course, secretions may be distributed by grooming (Hlavac, 1975a); a distinct, though unorganized cluster of grooming setae is present on the distal regions of the tibia.

Most of the enclosed surfaces of both head and mesothorax are covered with densely packed inclined scales or plates (figs. 1-7, 15). Those on the head project anteriorly, while the ones on the mesothorax are directed posteriorly. Both, therefore, are inclined towards the rim of the prothorax and

could form a barrier to the passage of foreign material. On the other hand, these plates could serve to store material secreted by glands located on the opposing, smooth, inner surfaces of the pronotum. This type of storage surface has been reported in the ant genus *Novomessor* by Hölldobler, Stanton and Engel (1976).

LARVAL MORPHOLOGY

The general form of a derodontid larva is illustrated by that of *Peltastica tuberculata* Mannerheim, shown in fig. 17. Superficially, it resembles that of various Cucujoidea, such as the nitiduline Nitidulidae, monotomine Rhizophagidae, or xenosceline Languriidae, but in more basic features, there is little to distinguish the larva from those of Eucinetidae or certain other primitive Polyphaga. The body is orthosomatic and slightly flattened, there are 6 well-defined ocelli, the entire dorsal surface is sclerotized and tuberculate, the urogomphi are well-developed, the first 8 abdominal tergites bear bifid median processes, the annular-biforous spiracles are borne on tubular processes, and the tenth segment is well-developed, rounded, and pygopod-like. The degree of dorsal sclerotization is much less in the other three genera of derodontids, median processes are replaced by one or more pairs of paramedian processes in *Derodontus* and *Nothoderodontus*, and are absent altogether in *Laricobius*, which also lacks urogomphi on tergite 9. There is variation in the development of spiracular processes (see generic key below) and in the size of the posteroventral ocellus (which is only vaguely indicated in *Nothoderodontus*).

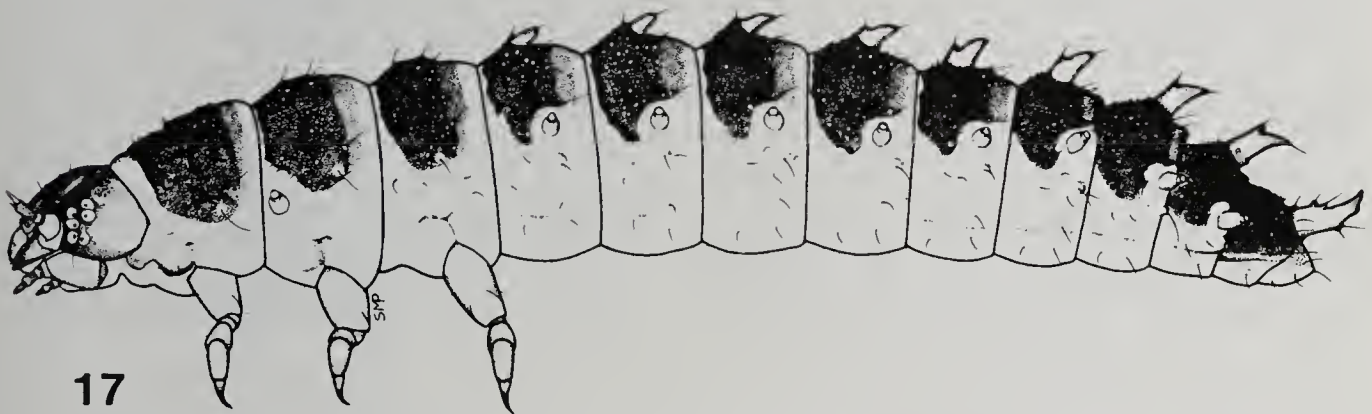


Fig. 17. Larva of *Peltastica tuberculata* Mannerheim, lateral view.

The head capsule is relatively short and broad, with a reduced gular region, retracted ventral mouthparts, and well-developed maxillary articulating areas. The epicranial stem is extremely short or absent, and the frontal arms are lyriform and complete to antennal insertions. The frontoclypeal suture appears to be present in all genera, but it is usually not well-defined. Antennae are 3-segmented, with a conical sensorium antero-ventrad of segment 3. The labrum is large and quadrate, with 2 longer and 4 shorter setae on the disc and a number of setae along the edge. The epipharynx has tormae which meet at the midline, where they are associated with a dense brush of posteriorly directed hairs; anteriorly the epipharynx bears a mesal, transverse row of sensilla and anterolateral patches of posteromesally directed hairs. The cibarial region bears a series of oblique, fringed plates, extending posterolaterally on each side of midline.

The mandibles are symmetrical with relatively flattened apices. In

Peltastica, *Derodontus*, and *Nothoderodontus*, each has a well-developed, tuberculate mola, dorsal and ventral patches of fine cuticular processes in oblique rows on either side of the mola, an accessory ventral condyle, an acute, sclerotized prosthema associated with a setal brush, and a relatively narrow incisor lobe with bifid apex. The rows of cuticular processes occur in a number of beetle larvae and have been described by Lawrence (1977:51) for the Pterogeniidae. Those on the dorsal surface fit tightly against the epipharynx, as seen in fig. 22, and they act in conjunction with cibarial plates to move small particles into the mouth cavity and away from articulating regions of the mandible. The ventral processes function in the same way in conjunction with the hypopharyngeal armature. The term "accessory ventral condyle" was used by Böving and Craighead (1931) and appears to be equivalent to the "ventral crushing tubercle" of van Emden (1942). It refers to a ventral process at the base of the mandible just laterad of the cuticular plates mentioned above and near the attachment of the adductor muscle. It is neither a condyle nor a crushing tubercle, but its function is not clear at present. The term prosthema (from the Greek *prostheke*, addition or supplement) is used here in the general sense to refer to any number of types of appendages (membranous or sclerotized, hyaline or pigmented, simple or complex, articulated or not) which may occur between the mola and the incisor lobe of the mandible. Those which are sclerotized, pigmented, and unarticulated are often called retinacula, although that term has also been applied to distinct incisor teeth in the larvae of Carabidae and Elateridae. In some Cucujoidea, the rigid and acute, but hyaline, lobe has been called both retinaculum and prosthema. The term "lacinia mobilis" has also been used, especially for an articulated prosthema. Variation in the prosthema and incisor lobe is described below. The mandible of *Laricobius* is highly modified, in that the mola is reduced, the prosthema is more rounded, and the incisor lobe is simple and acute at the apex.

The maxilla in *Peltastica*, *Derodontus*, and *Nothoderodontus* consists of two distinct lobes, an outer galea with a brush or setae at the apex and an inner lacinia bearing several stout setae along the inner edge and two or three teeth at the apex. In *Laricobius* the maxilla is also highly modified, with short rounded galea and lacinia which are not clearly separated from one another. The labium consists of a short, broad ligula and a complex hypopharyngeal region bearing patches of setae and parallel rows of cuticular plates; the hypopharyngeal sclerome consists of a flat, transverse plate, interrupted at the midline, and two anterior and posterior lateral struts. The hypopharyngeal region in *Laricobius* is also reduced.

Variation in the structure of the larval mouthparts appears to be correlated with differences in feeding habits, as is illustrated by the scanning electron micrographs of *Peltastica tuberculata* (figs. 18-20) and *Derodontus* sp. (Figs. 21-23). In *P. tuberculata*, which feeds on liquid fermenting material, the incisor lobe of the mandible (fig. 19) bears two rounded teeth perpendicular to the main axis and the prosthemal brush is well-developed. The maxillary galea (fig. 20) is larger than the lacinia and bears a well-developed apical brush. These are features which would be expected if the larva is feeding on material in liquid suspension, since the scoop-like mandibular apex and mandibular and maxillary brushes would aid in transporting soft material into the mouth cavity. *Derodontus* larvae feed on the reinforced hyphae comprising the fruiting bodies of a variety of higher Ba-



Figs. 18-20. Larva of *Peltastica tuberculata* Mannerheim. 18. Head, anterodorsal view. 19. Right mandible. 20. Left maxilla. Figs. 21-23. Larva of *Derodontus* sp. 21. Head, anterodorsal view. 22. Right mandible. 23. Left maxilla.

sidiomycetes, such a *Pleurotus*, *Hericium*, and *Ischnoderma*. The incisor lobe of the mandible (fig. 22) has a serrate edge and sharp apical teeth, while the prosthecal brush is reduced and not visible in dorsal view. The maxillary galea, on the other hand, is reduced with a smaller apical brush (fig. 23), while the lacinia is stouter with sharp apical teeth. This is the type of structure required to feed on a more solid matrix, which must be torn and shredded. The larva of *Nothoderodontus gourlayi* feeds on the bead-like hyphae of sooty molds and has coarse serrations on the incisor lobe of the mandible and somewhat reduced mandibular and maxillary brushes. The highly reduced mouthparts of *Laricobius* are correlated with the habit of preying on pine and spruce aphids (Adelgidae).

Larval legs in derodontids are moderately long and not especially modified, the tarsungulus bears two setae. The spiracles are always borne

on tubular processes, which vary in length, being longest in *Peltastica* and *Nothoderodontus*. The tenth abdominal segment is particularly well-developed in this family, being rounded, slightly sclerotized dorsally, and bearing four anal papillae.

Published Larval Descriptions. The larva of *Peltastica reitteri* Lewis was described and figured by Fukuda (1963), while that of *Laricobius erichsoni* Rosenhauer was described in detail by Franz (1958). The larva of a *Derodontus* species was keyed out and figured by Böving and Craighead (1931), while that of *Nothoderodontus gourlayi* was mentioned briefly by Crowson (1959), who noted that it was very similar to that of *Derodontus*, with a different number and arrangement of ocelli. A sixth ocellus was seen in our specimen of this larva, but it is reduced and difficult to make out.

Larval Material Examined. A few larvae of *Derodontus maculatus* were collected with adults in rotting fruiting bodies of *Pleurotus* sp. in Louisa, Kentucky. First and second instar larvae of *D. esotericus* were collected on fresh fruiting bodies of *Hericium* sp. in Red Oak, Oklahoma. Early instar larvae of *Derodontus* sp. were found in *Hericium coralloides* in Bar Harbor, Maine, and later instars of a *Derodontus* were taken at Rock Creek Park, Maryland (habitat unknown). *Peltastica tuberculata* larvae were taken in numbers, without associated adults, under bark of recently killed *Pinus* sp. at Blodgett Forest, El Dorado Co., California. A single larva of *Nothoderodontus gourlayi* was examined from a wet sooty fungus collected at Cowan Spur, near Baton River, South Island, New Zealand. A few examples of *Laricobius erichsoni* larvae were examined from Franz's original study material, made available through the Canadian Forest Service.

BIOLOGY

Habitat and Feeding Habits

Derodontids normally inhabit relatively humid forests, often in cooler regions, and with the exception of *Laricobius* species, which prey on adelgid Homoptera, they feed as both larvae and adults on various kinds of fungi or the products of fungal metabolism.

Peltastica appear to be restricted to fermenting sap flows or to those areas under the bark of relatively recently killed trees where bacterial or yeast fermentation is taking place. The placement of the spiracles at the ends of tubular processes is often characteristic of larvae occurring in this type of habitat; other examples may be found in the Nosodendridae and Nitidulidae. *Peltastica reitteri* has been collected on *Pterocarya rhoifolia* in Japan, while the North American *P. tuberculata* has been associated with *Pseudotsuga Menziesii* and a species of *Pinus* (Fukuda, 1963; Deyrup, in litt. see p. 402). As mentioned above, the mouthparts of both adult and larva have well-developed setal brushes, which are usually correlated with a diet of fine particles in suspension. The gut contents of a *P. tuberculata* larva collected under pine bark in California included a variety of cell types with several kinds of spores and hyphae.

The feeding habits of *Laricobius erichsoni* have been well documented by Franz (1958) and Clark and Brown (1958), while Clark and Brown (1960) have provided information on *L. rubidus*. Adults and larvae of these species feed on the so-called pine and spruce aphids belonging to the family Adelgidae (Chermesidae). The preferred host of *L. erichsoni* is the balsam woolly

aphid, *Adelges piceae* (Ratzeburg), which occurs on the trunks of *Abies* and *Picea*, but other hosts include *Adelges cooleyi* (Gillette); *Adelges nüsslini* (Borner), *Pineus pineoides* Cholodkovsky, and *Pineus strobi* (Hartig). *Laricobius erichsoni* has been introduced into the northwestern United States and the Canadian Maritime Provinces for the control of *Adelges piceae*. The native North American *L. rubidus* normally feeds on *Pineus strobi* on the trunks of eastern white pine (*Pinus strobus*) but it occasionally attacks *Adelges piceae* as well. According to Franz (1958), adult *Laricobius* feed primarily on adult adelgids, but may also take eggs and frequently have fungal hyphae and spores in the gut. Early instar larvae prefer eggs, while later instars take adults as well. The mechanics of feeding involve a piercing-sucking action with the aid of a pharyngeal pump.

Nothoderodontus gourlayi is associated with a sooty mold, known locally as fumagine, which occurs on the trunks of southern beech (*Nothofagus*) on the South Island of New Zealand. These fungi are placed in the family Capnodiaceae, an artificial assemblage of Ascomycetes, characterized by the dark colored, sooty mycelium consisting of bead-like hyphae (Wehmeyer, 1975). Crowson (1959) found these beetles beneath chips of bark encrusted with this fungus and often in areas moist from the sap flowing from a wound or with honey dew produced by Coccidae. Although the gut was not sampled in the single larva available to us, bead-like chains of dark cells were found adhering to the cuticle. Ecological data did not accompany the specimens of Chilean *Nothoderodontus*, but one individual of *N. chilensis* had a mass of dark, unidentifiable material in the gut, along with a few dark cells, 4-5 x 9-10 microns.

Members of the genus *Derodontus* feed on the fruiting bodies of a wide variety of higher Basidiomycetes. The following species have been recorded as hosts: *Claudopus nidulans*, *Pleurotus ostreatus*, *Pleurotus sapidus*, *Pleurotus* sp. (Tricholomataceae); *Pholiota squarrosa-adiposa* (Strophariaceae); *Bondarzewia berkeleyi* (Bondarzewiaceae); *Hericium coralloides*, *Hericium* sp. (Hericiaceae); *Merulius tremellosus*, *Phlebia radiata* (Corticaceae); *Inonotus dryophilus*, *Phaeolus schweinitzii* (Hymenochaetaceae); *Daedaleopsis nipponica*, *Fomitopsis pinicola*, *Ischnoderma resinosum*, *Scutigera ovinus* (Polyporaceae). Fresh fruiting bodies are preferred by the beetles, although they have been recorded from rotting mushrooms, "slimy fungus," and "watery fungus." According to Shepard (1976), larvae of *Derodontus maculatus* preferred stem and cap tissues of a mushroom and fed by rasping the tissue away with the mandibles and eventually excavating a small tunnel beneath the surface. Adaptations to this type of feeding—reduced setal brushes, serrate mandibular apex, and well-developed lacinia—have been described above and are illustrated in figs. 21-23.

Life Cycle Patterns

Because of lack of material, little can be said concerning the life cycles of *Peltastica* species. Fukuda (1963) found larvae of *P. reitteri* during April and May; he noted that the larvae were sluggish in their movements and that they entered the soil for pupation. *Peltastica tuberculata* larvae were collected in April and in late May. According to Lewis (1883), adults of *P. reitteri* were normally active in May and June, but could be collected as late as August. Our records for *P. tuberculata* are from April to June.

The life cycle of *Laricobius erichsoni* has been worked out in some detail by Franz (1958) for populations in Germany and by Clark and Brown (1958) for those introduced into eastern Canada. In Franz's study area near Munich, adults congregate on tree trunks about the middle of April, after hibernating in forest floor litter, and proceed to feed on adelgids and lay eggs. These adults die in June or July. The larval period is about two weeks, and the fourth instar larvae drop to the ground to pupate and emerge three or four weeks later in June or July as teneral adults, replacing the previous generation. These adults feed for some weeks or months on the *Adelges*-infested trunks and return to the forest floor from August to October (mainly during August). There is, then, a single generation per year, with the main feeding activities taking place from May through July, and adult dormancy occurring from August through the winter until April. Because of the early dormancy period, the species is unable to attack the fall generation of adelgids. Clark and Brown (1958) described a similar type of life cycle for the species in Canada but with the commencement of adult activity being later than in the European population (early May to late June with a peak in late May). The beginning of winter dormancy was also correspondingly earlier in Canada. Clark and Brown (1960) also studied the life cycle of *Laricobius rubidus* in New Brunswick and found that the spring emergence and oviposition period was somewhat earlier than in *L. erichsoni* from the same area (maximum adult activity from mid April to mid May). They also found a few 2nd and 3rd instar larvae in early August and postulated that there may be a complete second generation further south.

There appears to be little seasonality in *Nothoderodontus gourlayi*, based on records from Crowson (1959) and J. C. Watt (*in litt.*). Adults have been collected in the northern part of South Island, New Zealand in January, February, March, July, August, and November, although the largest series of adults and at least one larva were taken in summer. The two Chilean species were both collected in February on Chiloe Island.

The species of *Derodontus* have a unique type of life cycle, in that the majority of adult and larval activity takes place from late fall to early spring and the adult dormancy period occupies the entire summer. This is one of the reasons for the apparent rareness of these insects, as has been pointed out by Shepard (1976). Table 1 lists the numbers of adult collections for the four species of North American *Derodontus* for each month of the year. The total number of records is followed by the number based on more than two specimens. Collections of one or two specimens may possibly represent dormant animals picked up in the litter. Derodontid larval records exist for the two eastern species only, and some of these are not definitely associated with adults. There are two records for *D. esotericus*: one collection of 20 early instar larvae from Oklahoma, hatched from eggs laid in early December, and another series of about 50 early instar larvae collected in Maine in October and not associated with adults; both were from a species of *Hericium*. *Derodontus maculatus* is also known from two collections: two larvae collected in January in Oklahoma (Shepard, 1976) and three late instars collected on February 10 in Kentucky; both series were associated with adults of *D. maculatus*. Additional larvae of *Derodontus* sp. have been collected in January and February in Maryland by W. Shepard. Finally, there is a collection of about 35 larvae (both early and later instars) from Rock Creek Park, Maryland, collected according

to the label on "VI-4-1971" and not associated with adults. This information does not agree at all with the pattern suggested by the remaining records. The collector (W. Tyson) had been collecting in the area throughout the year, so the record is not necessarily the result of an error in recording the date. It is possible, however, that VI could have been XI which was mis-copied from field data.

If the life cycle pattern of *Laricobius* is considered to be more or less typical for temperate Coleoptera, then that of *Derodontus* involves a decided shift in activity period to the fall and winter months, with a relatively long adult dormancy period from about March to September. This may be misleading, however, since the historical change may have taken place in the other direction. Although winter activity is unusual in the Coleoptera as a whole, it is not necessarily a derived feature in this family. The geographic distribution of the entire group (northern Holarctic, southern Chile, southern New Zealand) suggests that the family may have originally been a cold adapted one. The summer activity of *Laricobius*, then, may be correlated with the evolution of predaceous habits and the necessity of synchronization with the life cycle of the host. As pointed out by Franz (1958), this synchronization is not complete in *Laricobius erichsoni*, and thus it is not as efficient a predator as the coccinellid *Scymnus impexus* (Mulsant).

TABLE 1. Adult Records for North American *Derodontus* (Numbers in parentheses are those records based on more than 2 specimens).

	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
<i>Derodontus esotericus</i>			1 (0)	1 (0)			2 (0)		4 (0)	13 (3)	7 (1)	4 (2)
<i>Derodontus maculatus</i>	6 (4)	4 (1)	2 (1)		1 (0)					6 (3)	5 (1)	3 (1)
<i>Derodontus trisignatus</i>		2 (0)							2 (1)	5 (4)	4 (1)	2 (0)
<i>Derodontus unidentatus</i>										6 (5)	2 (2)	

EVOLUTIONARY CONSIDERATIONS

Phylogenetic Relationships of the Family

Crowson (1944) called attention to the isolated position of derodontids by proposing the monotypic superfamily Derodontoidea. He later abandoned this position (Crowson, 1955, 1959, 1960) and united the family with Nosodendridae, Dermestidae, and Jacobsoniidae in the superfamily Dermestoidea. As Crowson himself recognized, however, the dermestoids are a paraphyletic assemblage which probably arose near the base of the Polyphaga and gave rise to the Bostrichoidea, as well as the large cucujiform lineage. There can be little doubt that the Derodontidae are very old and have been evolving independently for a long time. It is not surprising, then, that most of their features are either plesiomorphic or autapomorphic and thus of little use in determining sister group relationships.

Adult characters of the Derodontidae which appear to be primitive for

the Polyphaga as a whole include: (1) prothorax with membranous notosternal suture and remnant of anterior pleural fold (Hlavac, 1973); (2) prothoracic pleuro-coxal mechanism well-developed and normally exposed; (3) mesocoxa large and broadly open laterally meeting both mesepimeron and mesepisternum; (4) meso-metasternal joint lightly sclerotized; (5) transverse suture of metasternum present (6) hind coxae movable and excavate; (7) abdomen with a remnant of sternite 2; (8) abdominal segment 8 with functional spiracles; (9) segment 9 with complete sternite and divided tergite; (10) segment 10 present; (11) aedeagus of trilobed type with freely articulated parameres; (12) Malpighian tubules 6 in number and free. The paired ocelli on the head of derodontids may also represent a primitive condition, since similar structures occur in Hydraenidae and Staphylinidae. The meeting of mesocoxa and metepisternum occurs nowhere else in the Polyphaga but is the normal condition in Myxophaga and Archostemata; it is possible that its occurrence in derodontids is secondary. Primitive larval characters include: (1) mandible with accessory ventral process, tuberculate mola, and protheca; (2) maxilla with distinct galea and lacinia; (3) epipharyngeal, cibarial, and hypopharyngeal armature well-developed; (4) tarsungulus with 2 setae; (5) spiracles with a closing apparatus; (6) tenth segment well-developed. Cephalic egg bursters occur in the first instar larva of *Laricobius* and also in Hydraenidae, but little is known of their distribution in other beetle families. Autapomorphic characters include wing venation and folding, structure of the metendosternite, and numerous features of surface topography discussed above. The paired ocelli, mesocoxal condition, and cephalic egg bursters might well be added to this list.

Any attempt to place Derodontidae in a phylogenetic system must involve an understanding of Crowson's superfamily Dermestoidea, as well as the other three included families. Members of this group lack the diagnostic characters of Staphyliniformia, Elateriformia, and Cucujiformia, but are difficult to separate from the primitive Eucinetoidae, on the one hand, and the derived Bostrichoidea, on the other. As Crowson (1959) has stated, members of the Dermestoidea provide likely ancestors for both Bostrichoidea and Cucujiformia. We have not been able to find any consistently useful characters for uniting Derodontidae with dermestoids and separating the assemblage from the remaining Polyphaga, other than those already suggested by Crowson (1959) and van Emden (1951) and applying only to larvae. According to Crowson, dermestoid larvae have relatively heavily sclerotized and pigmented tergites and membranous sternites, while van Emden considered the spur-like lacinia of larval dermestoids to be diagnostic. Both characters may be used to distinguish Derodontidae from Eucinetidae, whose larvae in most respects are very similar. Adults of all eucinetoids may be distinguished from dermestoids by the distinctive type of head compaction, in which the prosternum is highly reduced and the head is flattened or concave ventrally, resting against procoxae, mesosternum or metasternum. In addition, most eucinetoids have filiform antennae and large, somewhat oblique metacoxae which are fused to the metasternum.

The large and varied cucujiform complex are distinguished from dermestoids by a suite of apomorphic characters, including non-excavate hind coxae; lack of functional spiracles on abdominal segment 8; cryptonephridial system in which Malpighian tubules are united independently with

the hindgut; cucujoid aedeagus, with the tegmen forming a ring around the median lobe; metendosternite derivable from the hylecoetoid type, described by Crowson (1938); and the undivided larval maxilla. Actually, the dermestoid Jacobsoniidae have non-excavate hind coxae, while the cucujiform Lymexylidae have an aedeagus resembling the dermestid type mentioned below.

Distinguishing dermestoids from bostrichoids is much more difficult, and it is here that the integrity of the former group appears to break down. The relationship of the family Dermestidae to members of the superfamily Bostrichoidea is based on several derived features, most of which do not occur in Derodontidae, Nosodendridae, or Jacobsoniidae. Dermestids and bostrichoids have a modified type of cryptonephridism, described by Saini (1964), in which all Malpighian tubules are attached in a bundle to one side of the hindgut. The dermestid aedeagus, which is found in bostrichoids (and also in lymexylids), has been described by Tandon (1970) and consists of a basal piece loosely attached to and somewhat overlapping the parameres, while the latter are fused dorsally at the base and attached at that point to the base of the median lobe. Other adult characters, such as the metendosternite, wing venation, and wing folding (Forbes, 1926), support this relationship. The larval mandible in Dermestidae always lacks a true basal, tuberculate or asperate mola, which is characteristic of the other dermestoid families; in all bostrichoids the mola is also absent. In the dermestid genus *Orphilus*, a small, non-tuberculate pseudomola is present, which is separated from the base of the mandible by a brush. This structure is remarkably similar to that found in primitive bostrichoids, such as *Endecatomous* and the Lyctinae, and constitutes further evidence for the relationship of Dermestidae to the bostrichoid complex. Bostrichoid larvae differ greatly from those of dermestids in general form, since they are specialized, grub-like borers.

The Nosodendridae appear to occupy a more or less intermediate position between Derodontidae and the dermestid-bostrichoid complex. The Malpighian tubules are free, as in derodontids, but the aedeagus is somewhat similar to the dermestid type. The basal piece is slightly overlapping and not distinctly articulated to the parameres, and the latter are connate but separated by a suture at the base and closely associated with but not attached to the median lobe. The metendosternite of *Nosodendron* is similar to that of dermestids, as is the wing venation and type of folding. Larvae of *Nosodendron* (Böving and Craighead, 1931, Hayes and Chu, 1946) resemble those of derodontids, particularly *Peltastica*, but most of the similarities (mandibular brush and basal mola, epipharyngeal and hypopharyngeal armature, spiracular tubes) are probably both plesiomorphic and associated with similar habitat and feeding habits (fermenting tree wounds).

The Jacobsoniidae have little in common with Dermestidae, except for certain primitive features, such as the complete abdominal apex with functional spiracles on segment 8, well-developed 9th tergite and sternite, and free 10th tergite. The wing venation, although somewhat reduced, is similar to that of Derodontidae and not at all to that of dermestids or *Nosodendron*; this type of wing, however, occurs in various Cucujoidea as well. The general form and non-excavate hind coxae of jacobsoniids is also suggestive of cucujoid affinities. The peculiar maxillary fringe in the larva resembles

that occurring in certain staphylinoids (Leiodidae), but this is almost certainly due to convergence. The aedeagus of *Saphophagus* and *Derolathrus* appears to be of a unique type, although the relationships of the parts are difficult to observe because of the small size; the median lobe appears to be completely surrounded by a sheath-like tegmen to which it is attached at the base. The metendosternite is reduced and could be derived from various other types, while the conditions of the Malpighian tubules is unknown.

The relationship of Dermestidae to Bostrichoidea seems to be well established, and there are several derived features which would include *Nosodendron* in the same group, in spite of its free Malpighian tubules and different larval mouthparts. The classification best reflecting such a phylogenetic hypothesis would involve the resurrection of Crowson's Derodontoidea and the inclusion of Nosodendridae and Dermestidae within the Bostrichoidea. Jacobsoniidae would have to be tentatively placed with the Derodontidae. The practical disadvantage of such a classification is the submersion of a relatively uniform and well-defined group as the Bostrichoidea; at the superfamily level, it represents the same kind of problem encountered when combining Cicindelidae and Carabidae or Lyctidae and Bostrichidae.

The Derodontidae is certainly a primitive family of Polyphaga and has probably evolved independently of any of the other lineages. Its most likely affinities are with Dermestidae via *Nosodendron* and with Cucujoidea via Jacobsoniidae.

Cladistic Analysis

In attempting to reconstruct a phylogeny of the Derodontidae, we are following the methodology first outlined by Hennig and discussed in detail in a number of recent papers (*see* Wiley, 1976: 7-13). The only point that needs emphasis here is that a phylogenetic analysis follows from the selection and delimitation of taxonomic characters. The selection process is particularly important in cladistic analysis, where many potential characters are rejected because they are judged to be plesiomorphic or because no decision can be made on the direction of evolutionary change. Taxonomic characters are, in turn, convenient artifacts, usually anatomical details, which are reflections of evolving functional systems. A failure to appreciate this can lead to the selection of characters which are superficial or which are taken out of context, without some thought being given to their geometric or functional relationships. Such a practice can only increase the chances of producing a phylogeny based on convergences or non-homologies. An example in derodontids involves the apomorphic condition "closed procoxal cavities", which refers to the external closure by the notum and sternum, forming a complete collar behind the coxae. This type of prothoracic collar has evolved numerous times in the Coleoptera and functions to permit extensive rotary movement of the prothorax while at the same time enclosing all pericoxal and intersegmental membrane (Hlavac, 1973). In *Peltastica*, narrow projections from the notum extend to the midline and meet behind the intercoxal process of the prosternum, the apex of which is not expanded. In *Derodontus*, the notal projections do not extend to the midline, but they slightly overlap the expanded apex of the intercoxal process. The chances are good that these represent two inde-

pendent evolutionary events and that the procoxal condition in derodontids must be more precisely defined.

Adult features considered to be plesiomorphic for the Derodontidae and thus present in the ancestral group include the following: (1) head with relatively fine punctation, without deep pores, canals or bridges; (2) ocelli small, round, close to eyes; (3) mandibles with well-developed, tuberculate mola and prostheca; (4) maxillae with well-developed galeal brush and 2 spines at apex of lacinia; (5) labium with glossae well-developed; (6) procoxal cavities open with trochantins exposed; (7) ventral surfaces finely punctate, without deep pores or canals; (8) metasternum with complete longitudinal and transverse sutures; (9) metepisternal interlocking device absent or weakly developed; (10) anterior processes of metendosternite rounded and not broadly meeting or fused at midline; (11) elytra with 11 rows of round punctures and with a scutellary striole; (12) abdomen without median ridges or tubercles; (13) hindwing with distinct radial cell, radial sector, long median vein, W cell, and 5 anal veins; (14) tibial spurs present; (15) tarsi not lobed. Larval features include: (a) sclerotized abdominal tergites with tubercles or processes; (b) well-developed mandibular mola, prostheca, and brush; (c) galea with large brush at apex; (d) lacinia with distinct apical teeth. Most of these features may be found in *Peltastica*, while certain of them occur only in *Derodontus* or *Laricobius*.

Each of the derodontid genera is quite distinct and has a number of autapomorphic characters, some of which are listed below.

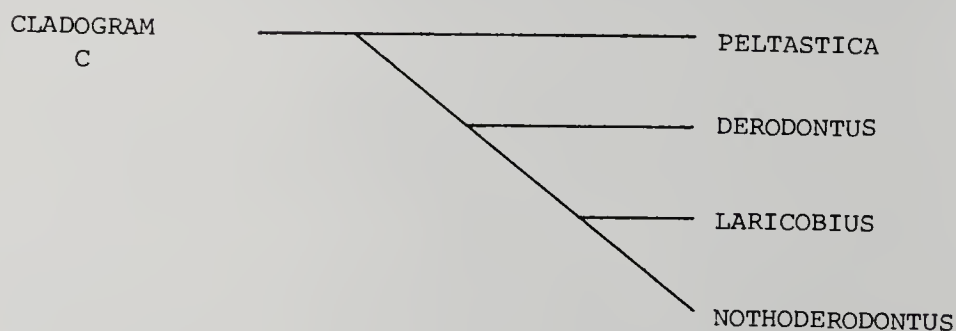
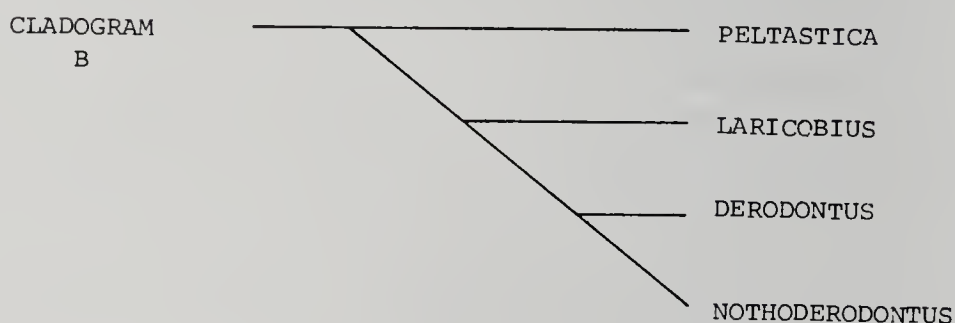
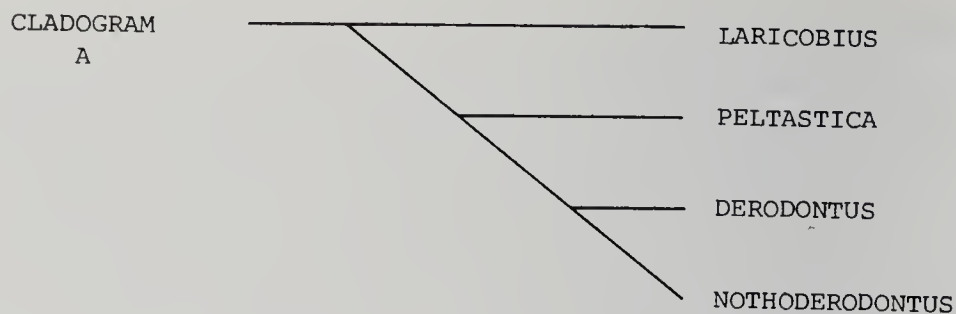
Peltastica: (1) concealed antennal insertions; (2) ventral antennal fossae; (3) explanate lateral margins to pronotum and elytra; (4) elytral seriation not distinct, 20 or more rows across each elytron; (5) procoxal cavities closed by meeting of notal projections at midline; (6) larva with median bifid processes.

Derodontus: (1) ocelli large and forming part of incomplete bridges; (2) unique system of head canals and bridges; (3) coarse, dense, ventral punctation; (4) modified elytral punctures with microbridges; (5) elongate, parallel-sided basal piece; (6) carinate median lobe; (7) larva with reduced galea and enlarged lacinia.

Laricobius: (1) shallow cavity, with deep invaginations, near antennal insertion; (2) two deep pores on mentum; (3) reduced mola, prostheca and subapical tooth on mandible; (4) reduced galeal brush; (5) single spine at apex of lacinia; (6) metendosternite with broadly fused anterior lobes, well-developed ventral process, and short lateral arms; (7) 10 elytral puncture rows; (8) lobed tarsal segments; (9) grooming comb and no spurs on tibia; (10) abdominal sternites 3 and 4 fused; (11) lateral canals and pores on abdomen; (12) larva without tergal processes or urogomphi; (13) larva with reduced mandibular mola and simple apex; (14) larva with highly reduced and rounded maxillary lobes.

Nothoderodontus: (1) vestiture of decumbent hairs; (2) unique system of head canals and bridges; (3) prothorax with concealed trochantins; (4) elytra without scutellary striole; (5) deep pores at bases of striae 9-11.

Of the 15 possible cladograms which can be constructed for the four genera of Derodontidae, two of them, (b) and (c) appear to us to be plausible hypotheses, while a third, (a) is that given by Fukuda (1963) and implied by Crowson (1955 and 1959). Cladograms (b) and (c) differ from (a) in considering the main cleavage to be between *Peltastica* and the remaining genera.



Crowson and Fukuda separated *Laricobius* from the remaining derodontids primarily on the basis of its numerous autapomorphic features (*see above*), many of which are correlated with its occurrence on surfaces and its predatory habits. A classification isolating *Laricobius* must be considered primarily a phenetic one. Aside from closed coxal cavities (which have been shown to be of two different types), there are few, if any, derived features that would unite *Peltastica* with *Derodontus* and *Nothoderodontus*. In cladograms (b) and (c), the following apomorphic characters are shared by *Laricobius*, *Derodontus*, and *Nothoderodontus*: (1) presence of a pair of median longitudinal ridges on the first visible sternite (segment 3); (2) well-developed anterolateral interlocking device on metepisternum, which fits into a notch in the elytron; (3) canal on the metacoxa; (4) reduction of wing venation; (5) more complex surface modifications associated with the secretion, distribution, and retention of cuticular exudate.

The choice between cladograms (b) and (c) is a more difficult one. *Derodontus* and *Nothoderodontus* share several apparently derived features, such as the system of head canals and bridges, distinctly hooked metepisternal interlocking device, overlapping meso- and metasternal intercoxal processes, and similar closure of the procoxal cavities (by expansions of both sternum and notum). Certain of these features need to be examined more closely. As indicated in the section on surface organization

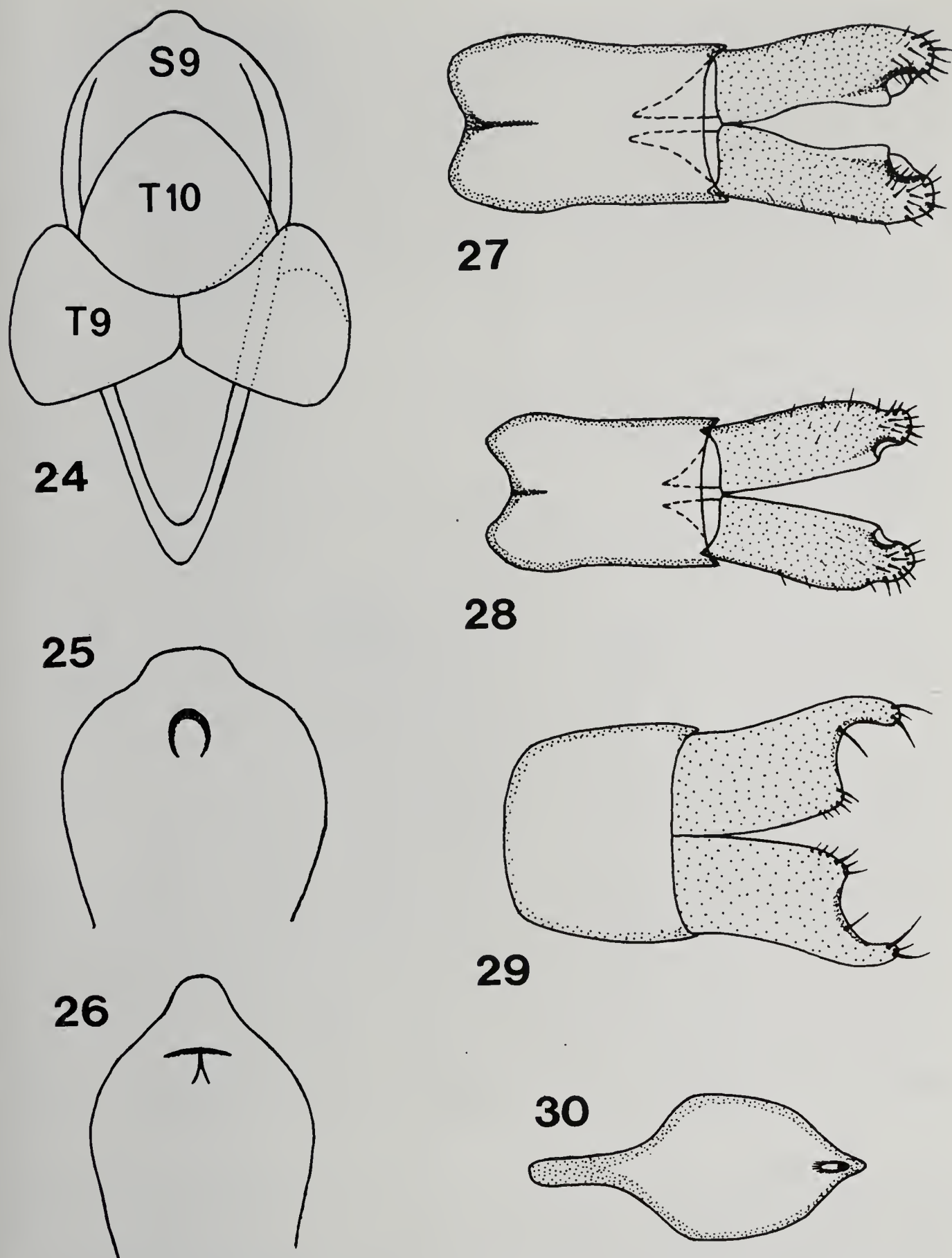


Fig. 24. 9th and 10th abdominal segments of *Derodontus esotericus*, n. sp., dorsal view. Figs. 25-26. Apex of 9th sternite. 25. *D. unidentatus*, n. sp. 26. *D. maculatus* (Melsheimer). Figs. 27-29. Basal piece and parameres, ventral view. 27. *D. maculatus*. 28. *D. esotericus*. 29. *Nothoderodontus gourlayi* Crowson. Fig. 30. Median lobe of *N. gourlayi*, ventral view.

(p. 379), the head canal systems in *Derodontus* and *Nothoderodontus* are not at all alike. In *Derodontus*, each ocellus forms part of three bievaginal bridges, two obliquely longitudinal ridges enclose a median frontal plain, and there is no deep frontoclypeal canal. *Nothoderodontus* has a series of connecting canals (including the frontoclypeal canal) without

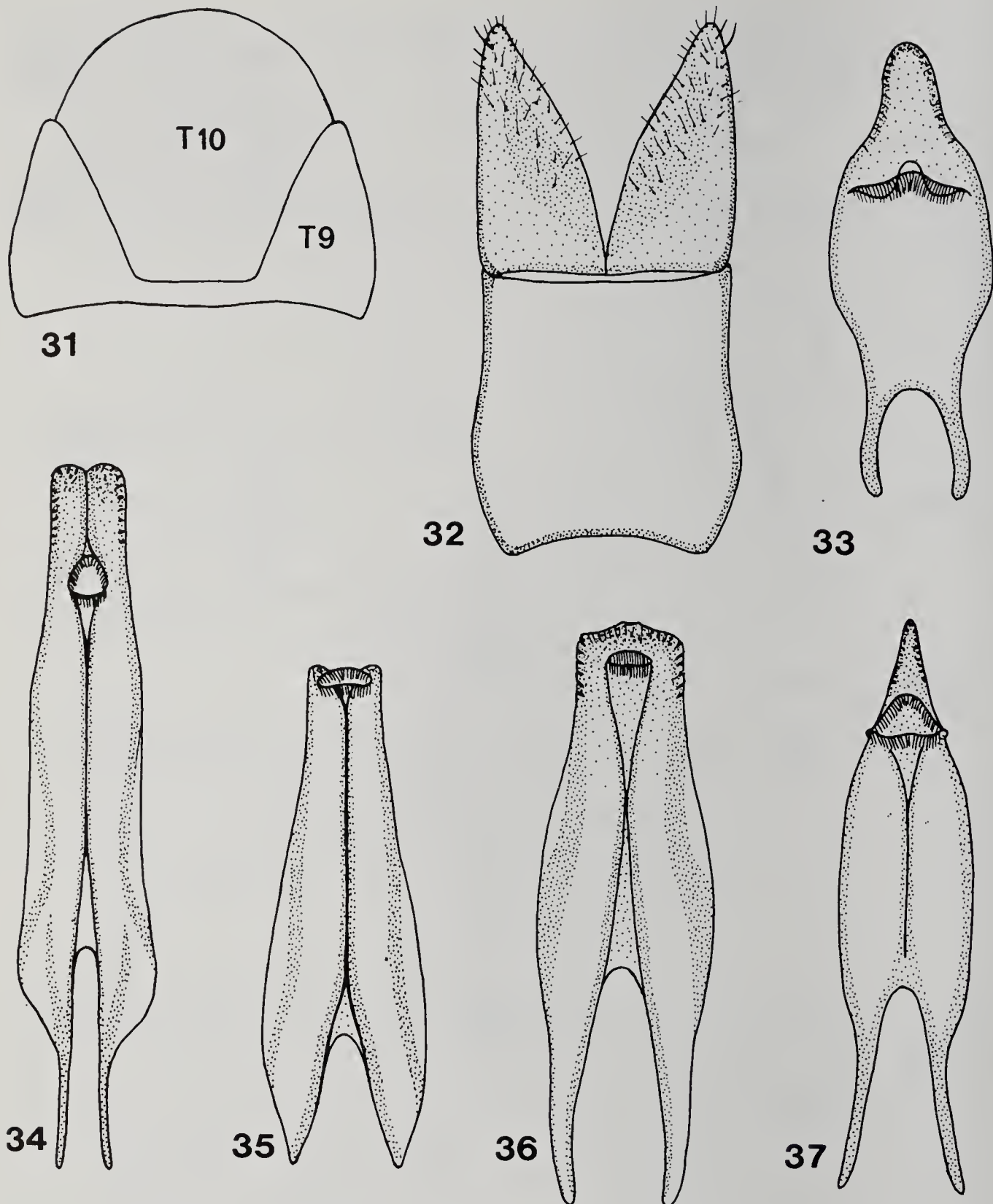


Fig. 31. 9th and 10th tergites of *Nothoderodontus gourlayi* Crowson. Figs. 32-33. Aedeagus of *N. dentatus*, n. sp. 32. Basal piece and parameres, ventral view. 33. Median lobe, ventral view. Figs. 34-37. Median lobe of *Derodontus* spp., ventral view. 34. *D. maculatus* (Melsheimer). 35. *D. esotericus*, n. sp. 36. *D. trisignatus* (Mannerheim). 37. *D. unidentatus*, n. sp.

evaginated ridges, and the ocelli are not incorporated into bridges. The closure of the procoxal cavities also differs in the two genera. In *Derodontus*, the notal projection is narrower, leaving the trochantin exposed, while in *Nothoderodontus* the trochantin is entirely concealed by the notal projection.

A close relationship between *Laricobius* and *Nothoderodontus* has not been previously suggested, but there seems to us to be some evidence in favour of it. The major derived feature shared by these two genera is the sys-

tem of pores and canals more or less surrounding the mesocoxal cavities and located on the mesosternum, mesepisternum, metepisternum, and metasternum. These pores are similarly placed in the two genera and could represent homologous systems. In *Derodontus*, the ventral surfaces are entirely different, with no specialized deep pores, but with more or less evenly distributed large, shallow punctures, which are somewhat clustered on the metepisternum (Fig. 8), forming a shallow depression. The vestiture in both *Laricobius* and *Nothoderodontus* consists of long hairs, and setae are present among the eye facets; in *Derodontus*, the surface is almost glabrous, with minute hairs occurring in the punctures and no setae among the eye facets.

Cladogram (c) would involve the independent closure of procoxal cavities, meso-sternal overlap, metepisternal hook, and analogous head canal systems; cladogram (b) would require the independent development of a meso-metathoracic pore system, as well as the ocular setae and vestiture of long hairs. Given the differences in the procoxal closure and head canal systems of *Derodontus* and *Nothoderodontus*, it appears to us that they are much more likely to be convergent than are the meso-metathoracic pore systems of *Laricobius* and *Nothoderodontus*. On the other hand, both hypotheses are based on limited evidence, and the discovery of new taxa or additional characters might well tip the balance one way or another. In the classification presented below, only the first bifurcation (Peltasticinae/Derodontinae) is formally recognized.

Phylogenetic relationships within the genera *Peltastica*, *Derodontus*, and *Laricobius* have not been studied in detail, since we have been unable to examine most of the Old World species. Within *Derodontus*, however, the two western North American species, *D. tridentatus* and *D. unidentatus* appear to form a distinct group which is related to the Old World forms. The European *D. macularis* may be more primitive than any of the North American species, since the elytral punctures are rounded and do not have microbridges. Among the species of *Nothoderodontus*, the two Chilean forms appear to be more primitive than the New Zealand and Australian species, and the head canal system of the latter can be derived from that of the former (see p. 379). The aedeagus of *N. gourlayi* is also highly modified, and that in the Chilean species has simple, subacute parameres resembling those of some *Laricobius* (see Figs. 29-30 and 32-33).

Historical Scenario

To date there have been no fossil Derodontidae described, although Ponomarenko (1973) has implied their presence among early Jurassic material. It is also possible that certain described Archostemata (Ponomarenko, 1969) may be early members of this family. The development of the propleuron varies considerably among fossil specimens and is often difficult to observe. The condition of the mesocoxal cavities (closed partly by the metepisterna) occurs in Derodontidae, as well as in Archostemata, and the *Derodontus* type of elytral punctation with incomplete microbridges and a scutellary striole can be seen in a number of fossil archostematans. At any rate, on the basis of primitive family characters described in the previous sections, as well as the considerable diversity within the group and its

relict type of distribution, the Derodontidae may be considered to be among the oldest of the Polyphaga, along with the eucinetoids, dascillids, and primitive staphylinoids.

The ancestral habit of derodontids may well have resembled those of modern *Peltastica*, with the food consisting of fermenting material, fungi, and fungal by-products in a more or less liquid medium. This is also the type of habitat in which some eucinetids, helodids, and leiodids are found. *Peltastica* may have developed hidden antennal insertions, antennal fossae, and explanate lateral margins in connection with living under bark, but such features would also serve as protection while on bark surfaces. The long spiracular tubes and setose mouthparts of the larvae appear to be correlated with a semi-liquid environment, such as that encountered in fermenting cambium. The ancestral form would also have developed a generalized encrusting system such as that found in *Peltastica*, with a repellent or fungicidal exudate being produced by unspecialized surface pores.

If we accept hypothesis (c) above, the next bifurcation would have produced one lineage leading to *Derodontus* and another to the ancestor of both *Laricobius* and *Nothoderodontus*. In each line, the generalized encrusting system would have been elaborated upon in different ways. In *Derodontus* complex head topography and modified elytral punctures were developed, while members of the second lineage developed a series of pores and canals on the ventral surfaces. In the *Derodontus* line, a switch in feeding habits occurred and the larval mouthparts were modified for handling the hyphae of basidiomycete fruiting bodies (see p. 384). Adults developed a complete prothoracic collar, which perhaps assists in tunneling the surfaces of macrofungi.

The ancestor of *Laricobius* and *Nothoderodontus* would have retained certain primitive characters, such as the open procoxal cavities in the adult and larval feeding habits similar to those of the ancestral derodontid. Feeding on sooty molds would represent a relatively small change from the ancestral habit, and since these fungi are often associated with honeydew-producing Homoptera, it is easy to conceive of a predaceous line evolving at this point. Both *Laricobius* and *Nothoderodontus* are associated with the bark of trees, the latter preying on adelgids and the former feeding on sooty mold spores. *Nothoderodontus* evolved, independently of *Derodontus*, a system of head canals and pores, in addition to a unique type of elytral striation and a closure of the procoxal cavities involving the concealment of the trochantins by the notal cowlings. *Laricobius*, on the other hand, retained a relatively primitive head structure, except for the cavities associated with antennal insertions, while evolving highly modified, lobed tarsi, often correlated with activity on plant surfaces, as well as a predaceous type of feeding mechanism in both larva and adult.

The present day distribution of derodontids suggests that they evolved primarily on the Laurasian land mass, but at some point before the breakup of Pangaea, their range must have extended through the Archiplatan region to what is now southern South America (see Schlinger, 1974). Evolution on the southern continent gave rise first to the *Nothoderodontus chilensis* group and then to the *N. gourlayi* complex on Australia and New Zealand. If our phylogenetic hypothesis is correct and *Nothoderodontus* is the most recently derived genus, then we must assume that the northern elements evolved by the middle of the Triassic.

SYSTEMATICS

Family Diagnosis

With the general characters of Coleoptera: Polyphaga.

Adult. Size small, length from 1.5 mm to almost 4 mm; more or less elongate, dorsally convex and ventrally flattened; vestiture of short, fine hairs or longer, erect or decumbent hairs. Head with 2 ocelli; compound eyes relatively large and entire; antennae 11-segmented with 3-segmented club, insertions concealed or exposed; frontoclypeal suture absent; frons and vertex sometimes with a complex system of pores, canals and bridges; labrum well-developed. Mandible with well-developed mola and prostheca, except in *Laricobius*; maxilla with brush-like galea and lacinia bearing 1 or 2 spines at apex; palp 4-segmented, apical segment subulate; labial palps 3-segmented. Prothorax relatively small with sides often explanate, at least at middle, and edges complete and usually dentate; prosternum relatively short in front of coxae, with narrow intercoxal process; notosternal joint membranous; procoxae conical and projecting below sternal process, bent at apex; trochantin exposed or concealed, pleuron rigid; cavities open internally, externally open or closed. Mesocoxae approximate to almost contiguous; cavities broadly open laterally, bordered by both mesepimeron and metepisternum; perimeter of each cavity sometimes with several deep pores. Elytra seriate or striate (except in *Peltastica*), with 10 or 11 puncture rows or striae; scutellary striole present or absent. Metasternum with long median suture and with transverse suture, which may be interrupted or incomplete; anterolateral portion of metepisternum with elytral interlocking device; metacoxae somewhat motile, approximate, extending laterally to rim of elytra, with weakly developed plates. Metendosternite with stalk short, median process well-developed, anterior tendons close together, and lateral arms narrow and curved. Hindwing with long membrane, distinct stigma, and interrupted costal margin; radial cell short and vague or absent; radial sector short, oblique, attached to radio-medial crossvein; median vein relatively short; anal venation more or less reduced, but jugal lobe distinct. Legs relatively short; trochanter obliquely attached to femur; tibial apex with 2 small spurs, except in *Laricobius*, which has apical comb; tarsal segmentation 5-5-5, segments simple, except in *Laricobius* where 1-3 are lobed; claws simple. Abdomen with 5 visible sternites (segments 3-7) and trace of segment 2 concealed beneath coxae; all segments free, except in *Laricobius* where 3 and 4 are connate; longitudinal ridges sometimes present on sternites 3-6 and lateral pores and canals present in *Laricobius*; segments 8-10 enclosed; segment 8 with functional spiracles; segment 9 well-developed with 2 hemitergites, which may be fused at midline; tergite 10 free. Aedeagus of simple trilobed type, with basal piece articulated to separate parameres and median lobe free. Ovipositor short, with 1-segmented coxites and short styli (longer sclerotized styli in *Derodontus*). Malpighian tubules free, 6 in number.

Larva. Elongate, subcylindrical to slightly flattened; dorsal surfaces sclerotized and tuberculate, often with median processes or paired tubercles. Head prognathous; epicranial stem very short or absent; frontal arms more or less approximate at base, lyriform and complete; median endocarina absent; ocelli 6 on each side; frontoclypeal suture vaguely defined; antennae 3-segmented, relatively long, with segments 2 and 3 elongate and anteroventral sensorium on segment 2; labrum free. Mandibles symmetrical, unidentate or bidentate, with well-developed, tuberculate mola and prostheca, reduced in *Laricobius*; ventral tubercle present. Maxillae with brush-like galea, spur-like lacinia, and well-developed articulating area; palp 3-segmented; maxillae highly reduced in *Laricobius*. Labium with broad ligula and 2-segmented palps. Epipharyngeal, hypopharyngeal, and cibarial areas often with rows of spines and complex armature. Legs moderately long, not specially modified; tarsungulus with 2 setae. Tergite 9 with pair of solid urogomphi; segment 10 well-developed, terminal, sometimes sclerotized dorsally. Spiracles annular-biforous, sometimes borne on tubular processes, with closing apparatus.

Key to Genera of Derodontidae (Adults and Larvae)

1. *Adult.* Antennal insertions concealed from above; ocelli very small, round, touching inner margin of eye; sides of pronotum and elytra strongly explanate and flattened, the edges of both slightly serrate; elytra tuberculate, each with about 20 irregular rows of punctures; first visible sternite simple. *Larva.* Abdominal tergites 1-8 each with median bifid process (Fig. 17); apex of galea with dense brush of setae, that of lacinia with 3 teeth or lobes, more or less equal in size (Fig. 20); mandible with dense brush of setae around prostheca (Fig. 19); upper surface heavily pigmented, granulate, and tuberculate; spiracular processes well-developed, at least as long as pleural processes beneath them *Peltastica* Mannerheim
- 1'. *Adult.* Antennal insertions exposed; ocelli larger and not touching eye margin; sides of pronotum, but not elytra, slightly to moderately explanate, the edges smooth or dentate; elytra without tubercles, each with 10 or 11 puncture rows or striae; first visible sternite with 2 longitudinally parallel ridges near midline (Fig. 8). *Larva.* Abdominal tergites 1-8 without median bifid processes, with or without one or more paired processes; apex of galea with few or no setae, that of lacinia, if dentate, with only 2 well-developed teeth and sometimes a smaller, subapical one (Fig. 23); prosthecal brush reduced or absent (Fig. 22); upper surface not as heavily pigmented and less granulate; spiracular processes variable 2
- 2(1'). *Adult.* Dorsal surface clothed with moderately long, erect hairs; lateral edges of pronotum smooth; each elytron with scutellary striole and 10 rows of round punctures; tarsal segments 2 and 3 strongly lobed, segment 4 reduced; procoxal cavities open behind; head (Fig. 7) without canals and bridges. *Larva.* Abdominal tergite 9 without urogomphi; mandibular mola reduced, not extending to base of mandible, incisor lobe simple; galea and lacinia rounded at apex *Laricobius* Rosenhauer
- 2'. *Adult.* Dorsal surface subglabrous or with recumbent hairs; lateral edges of pronotum slightly to strongly dentate; each elytron with 11 rows of modified punctures, with or without scutellary striole; tarsal segments 2 and 3 not lobed; procoxal cavities closed behind; head (Figs. 1-4) with canals and bridges. *Larva.* Abdominal tergite 9 with a pair of urogomphi; mandibular mola well-developed, extending to base of mandible, incisor lobe serrate; galea and lacinia falciform, the latter dentate at apex 3
- 3(2'). *Adult.* Dorsal surface subglabrous, with a few scattered, fine setae; each elytron with scutellary striole and 11 rows of punctures, each of which may be somewhat quadrate and narrowed in middle; undersurface covered with large, shallow punctures (Fig. 8); prothorax with visible trochantin; visible sternites 2-4 with median longitudinal ridge or tubercle; ocelli large, triangular, each connected to 2 cuticular bridges

(Figs. 1-2); frontal region bounded laterally by 2 oblique ridges. *Larva*. Abdominal tergites 1-8 each with a single pair of larger setiferous processes and 1 or more pairs of smaller tubercles; spiracular processes not as well-developed, usually shorter than the pleural processes beneath them; incisor lobe of mandible with 8-10 fine serrations. Holarctic species....

- *Derodontus* LeConte
- 3'. *Adult*. Dorsal surface clothed with recumbent hairs; each elytron with 11 rows of elongate punctures which are situated within impressed striae, scutellary striole absent; under-surface finely punctate, but with deep pores on meso- and metepisterna and anterior edge of mesosternum (Figs. 15-16); prothorax without visible trochantin; visible sternites 2-4 simple; ocelli more rounded and not connected to cuticular bridges (Figs. 3-4); frontal region without lateral ridges. *Larva*. Abdominal tergites 1-8 each with 3 pairs of setiferous processes, more or less equal in size; spiracular processes well-developed, usually longer than pleural processes beneath them; incisor lobe of mandible with 3-4 coarse serrations. Southern Hemisphere species..... *Nothoderodontus* Crowson

Subfamily Peltasticinae LeConte

Peltasticidae LeConte, 1861:88.

Peltastica Mannerheim

Peltastica Mannerheim, 1852:334. Type species, by monotypy, *P. tuberculata* Mannerheim.

The three included species are easily distinguished from other derodontids by the very broad, explanate, lateral margins on the pronotum and anterior portion of the elytra, concealed antennal insertions, and tuberculate elytral surface, bearing about 20 irregular puncture rows.

Distribution. Northwestern North America, Japan, and the Amur Region of the U.S.S.R.

Biology. Both *P. tuberculatus* and *P. reitteri* have been found in association with fermenting sap under bark or at the ends of freshly cut stumps or logs (Lewis, 1883; Fukuda, 1963; Deyrup *in litt.*).

Peltastica amurensis Reitter

Peltastica amurensis Reitter, 1879:220. Type locality: Amur.

According to the figure of Jacobson (1907), this species resembles *P. reitteri* in form and coloration, but the comments made by Lewis (1883) indicate a greater similarity to the American *P. tuberculata*.

Peltastica reitteri Lewis

Peltastica reitteri Lewis, 1883:79. Type locality: Japan (types from Suyama, Nikko, and Fukui).

This species may be distinguished from *P. tuberculata* by the shorter and broader elytra (EL/EW about 1.4, as compared to 1.5 or more), relatively straight lateral pronotal margins, somewhat coarser and denser pronotal punctation, and differently shaped prothorax, the sides of which diverge from the apex to the basal third and are broadly rounded posteriorly.

Biology. See 386 and 387.

Peltastica tuberculata Mannerheim

Peltastica tuberculata Mannerheim, 1852:334. Type locality: Sitka Island [Baranof Island], Alaska.

Individuals of this species are more elongate and narrow, the sides of the elytra are slightly sinuate, the pronotal punctation somewhat finer and sparser, and the sides of the pronotum divergent from the apex to the basal fourth and more abruptly narrowed posteriorly. The color is usually brownish above with black tubercles, yellow spots, and a large, V-shaped yellow macula crossing both elytra at the anterior fourth.

Distribution. Southern Alaska, western British Columbia, Washington, and Oregon, southwestern Idaho, and California at least into the northern Sierra Nevada (El Dorado Co.) (Hatch, 1962).

Biology. Deyrup (*in litt.*) found adults in western Washington feeding on fermenting sap from the cut end of a *Pseudotsuga Menziesii* log in late April and collected a single larva under the bark of a year-old cut stump; a strong odor of fermentation was noted in the latter habitat. J. T. Doyen collected a number of larvae (not reared but compared with specimens sent by Fukuda) in late May under the bark of *Pinus* sp. killed less than a year earlier at Blodgett Forest in the Sierra Nevada.

Subfamily Derodontinae LeConte

Derodontidae LeConte, 1861:100.

Laricobiidae Ganglbauer, 1899:766.

Derodontus LeConte

Derodontus LeConte, 1861:100. Type species, by present designation, *Cryptophagus maculatus* Melsheimer.

Mycetomychus Frivaldsky, 1865:192. Type species, by monotypy, *Corticaria macularis* Fuss.

Members of this genus are distinguished by the subglabrous dorsal surface, 11 distinct rows of large elytral punctures and a scutellary striole, and large, somewhat triangular ocelli, each of which is connected to 2 cuticular bridges. The lateral edges of the pronotum are armed with well-developed teeth, and the ventral surface bears a number of large punctures.

Distribution. Southeastern Europe, Italy, eastern half of North America, northwestern North America, Japan.

Biology. Both adults and larvae have been taken in association with a variety of higher basidiomycete fungi (Agaricales, Polyporales, etc.), where they feed on or just under the surface of fresh or rotting fruiting bodies. See pp. 387 and 388.

Key to North American Species of Derodontus (Adults)

1. Sides of pronotum narrowly expanded (Figs. 11-12); elytra more than 1.7 X as long as the greatest combined width, each with a large, dark macula; head (Fig. 2) with complete transverse ridge, distinct median boss, and smooth frontal area; western North America 2
- 1'. Sides of pronotum more broadly expanded (Figs. 9-10); elytra less than 1.7 X as long as greatest combined width, each with a number of dark spots of varying size and shape; head (Fig. 1) with transverse ridge incomplete at middle, median boss indistinct, and frontal area rugose or tuberculate; eastern North America 3
- 2(1). Sides of pronotum (Fig. 12) subparallel and barely expanded, each with a prominent, posteriorly curved tooth at anterior end; elytral intervals flat; median lobe acute at apex (Fig. 37) *D. unidentatus*, n. sp.
- 2'. Sides of pronotum (Fig. 11) strongly curved and distinctly but narrowly expanded, each with several small teeth, none of which curves posteriorly; elytral intervals convex, median lobe obtusely angulate at apex (Fig. 36) *D. trisignatus* (Mannerheim)
- 3(1'). Sides of pronotum (Fig. 10) each with prominent, posteriorly curved tooth at apical third; parameres (Fig. 27) each with larger and more abrupt mesal notch near apex; median lobe (Fig. 34) 1.4 X as long as basal piece, with long basal struts....
..... *D. maculatus* (Melsheimer)
- 3'. Sides of pronotum (Fig. 9) each with several shorter teeth, none of which curves posteriorly; parameres (Fig. 28) each with smaller and less abrupt mesal notch near apex; median lobe (Fig. 35) 1.1 X as long as basal piece, with short basal struts.....
..... *D. esotericus*, n. sp.

Derodontus esotericus Lawrence, **new species**
(Fig. 9)

This species is distinguished from *D. trisignatus* and *D. unidentatus* by the expanded sides of the pronotum, shorter and broader elytra with finer maculations, and head with an incomplete transverse ridge, indistinct boss, and rugose frontal area. It differs from the broadly sympatric *D. maculatus* in lacking the prominent, posteriorly curved tooth on each lateral edge of the pronotum and in genitalic characters, such as the shorter median lobe and less abruptly notched parameres.

Description. Length 1.8-2.7 mm. Color of head and pronotum yellowish brown to dark reddish brown; elytra yellow with variable black or brown markings, usually including the anterior fourth of suture, anterior portion of third elytral interval, a spot on each side of suture at anterior fourth, extending from first to third puncture row, and various spots or maculae laterad and posterad of these, but excluding posterior fourth of disc. Head (Fig. 1) with subcircular, convex, median boss, not wider than the length of an ocellus, bordered posteriorly by shallow and poorly defined trough; median ridge narrowed and incomplete in middle; anterior bridges

very narrowly meeting; frontal area somewhat tuberculate or rugose. Pronotum about 0.85 X as long as wide at middle, sides strongly curved and broadly expanded, each with from 5 to 8 relatively small teeth, none of which curve posteriorly. Elytra about 1.6 X as long as greatest combined width and 3.4 X as long as pronotum; elytral intervals convex, with distinct carinae being formed at anterior ends of at least 3rd, 4th, and 5th. Sternite 9 of male with vague longitudinal carina near apex; parameres (Fig. 28) 0.87 X as long as basal piece, each with indistinct metal notch near apex; median lobe (Fig. 35) blunt and slightly emarginate at apex, 1.1 X as long as basal piece, with short basal struts.

Types. Holotype, male, Audubon State park, West Feliciana Par., LOUISIANA, Dec. 5, 1965, Lot 1647 J. F. Lawrence, ex *Claudopus nidulans* [MCZ 32364]. Paratypes: ALABAMA: 1, Mobile, Dec., 1921, (H. P. Löding) [MCZ]; ARKANSAS: 1, Queen Wilhelmina State Park, 2500' Polk Co., Oct. 11, 1974, gilled mushrooms on dead log (A. Newton) [MCZ]; DISTRICT OF COLUMBIA: 1, Rock Creek, Dec. 6, 1900 [USNM]; 1, Washington, Oct. 28 (H. S. Barber) [USNM]; ILLINOIS: 3, no specific locality [MCZ]; INDIANA: 4, no specific locality [MCZ]; IOWA: 1, Iowa City, Oct. 10, 1896 (Wickham) [USNM]; 1, same locality (Wickham) [AMNH]; LOUISIANA: 33, same data as holotype [CAS, FMNH, JFL, MCZ]; MARYLAND: 2, Laurel, 1966, Lot 1959 J. F. Lawrence (O. K. Miller), ex *Merulius tremellosus* [MCZ]; 1, Plummers Is., Nov. 8, 1905 (E. A. Schwarz) [USNM]; 1, same locality, Oct. 28, 1913 (R. C. Shannon) [USNM]; MASSACHUSETTS: 1, Arl[ington], Nov. 18 (P. J. Darlington) [MCZ]; 2, Drac[ut], Oct. 25, 1885 (F. Blanchard) [MCZ]; 1, Holliston, Oct. 20 (N. Banks) [MCZ]; 1, Lowell (H. C. Fall) [MCZ]; 7, Tyngs[boro] (F. Blanchard) [MCZ]; 5, no specific locality (F. Blanchard) [MCZ]; NEW HAMPSHIRE: 3, North Conway, Carroll Co., Oct. 3, 1971, Lot 3301 J. F. Lawrence (C. R. Hammond), ex *Scutigera ovinus* [MCZ]; 2, no specific locality, Sept. 24, 1889 (H. C. Fall) [MCZ]; NEW YORK: 2, Canton, Sept. 28, 1935 [MCZ, USNM]; 1, 5 mi. SE Bluffton, Wells Co., Oct. 24, 1974, fungus on *Fagus* (R. F. Wilkes) [CDA]; 1, Elbridge, Sept. 14, 1940 (N. Downie) [MCZ]; 1 same locality, Apr. 7, 1941 [FMNH]; 1, Esopus, Oct. 27, 1888 (F. C. Bowditch) [MCZ]; 1, Pike, Sept. 16, 1901 [MCZ]; 3, same locality, Oct. 11, 1901 [MCZ]; 2, same locality, Nov. 11, 1909 [FMNH]; 1, Pompey, Onandaga Co., Oct. 16, 1968, Lot 1866 J. F. Lawrence, ex *Phlebia radiata* [JFL, MCZ]; 5, Staten Is., Nov. 8, 1904, (E. Shoemaker) [USNM]; 2, Valhalla, Nov. 12, 1916, on slime mold-decaying logs (F. M. Schott) [AMNH]; NORTH CAROLINA: 1, Boardman, *Pinus* 3345b Hopkins U.S. (W. F. Fiske) [USNM]; 3, no specific locality (F. C. Bowditch) [MCZ]; OHIO: 1, Marietta, 10.11.74, J. LeConte Collection [MCZ]; 1, no specific locality (W. G. Dietz) [MCZ]; OKLAHOMA: 5, Red Oak, Latimer Co., Dec. 1, 1976, Lot 4167 J. F. Lawrence (K. Stephan), ex *Hericium* sp. [JFL, MCZ]; ONTARIO: 2, Tilbury, July, 1967 (K. Stephan) [CNC]; 4, Toronto [MCZ]; 6, Wheatley, Oct. 16, 1967 (K. Stephan) [CNC]; 3, C[anada] W[est] [MCZ]; 4, no specific locality [CNC]; PENNSYLVANIA: 1, Bethlehem, Nov. 8, 1903 (G. W. Caffrey) [USNM]; 6, Allegheny (J. B. Smith) [USNM]; 1, Frankford, Nov. 14 (G. M. Greene) [USNM]; 1, no specific locality, G. Horn Collection [MCZ]; TEXAS: 2, Fedor (H. C. Fall) [MCZ]; VIRGINIA: 1, Dead Run, Fairfax Co., Mar. 13, 1915, under bark dying tulip tree (R. C. Shannon) [USNM]; 2, no specific locality (C. V. Riley) [USNM]; CANADA (no other data): 7, G. Horn Collection [MCZ]; 2, [MCZ].

Distribution. Eastern North America from southern Ontario to Alabama and west to Oklahoma and Texas.

Biology. Adults have been taken on *Claudopus nidulans*, *Merulius tremellosus*, *Scutigera ovinus*, and *Phlebia radiata*. Larvae and adults were collected on *Hericium* sp. in Oklahoma.

Derodontus japonicus Hisamatsu

Derodontus japonicus Hisamatsu, 1964:52. Type locality: Mt. Sara, 1,200 m., Ehime Pref., Japan.

From the description and figures, this species appears to be similar to *D. macularis* and *D. trisignatus* in the form of the pronotum, while differing from both in the details of the elytral pattern.

Biology. A large series of adults were collected in the fruiting body of *Daedaleopsis nipponica*.

Derodontus macularis (Fuss)

Corticaria macularis Fuss, 1850:127. Type locality: Kerceschora?, Rumania.

This species has an elytral pattern similar to that of *D. maculatus* and *D. esotericus* but differing in detail (anterior part of suture not pigmented, posterior two-fifths of suture crossed by two oblique maculae). The elytral intervals each bear a row of distinct setae, which are about as long as a puncture diameter and easily visible at 40 X magnification. In all of the North American species these setae are absent or extremely short. The pronotum of *D. macularis* resembles that of *D. trisignatus* and *D. japonicus* in being relatively narrowly explanate and bearing several small teeth on each side. The transverse ridge on the head is very strongly curved, and the median boss is barely indicated.

Distribution. Known primarily from the mountains of southeastern Europe.

Biology. Dorn (1936) collected this species on the fruiting bodies of *Ischnoderma resinosum* in the Bohemian Forest (Czechoslovakia). It has also been recorded from soft, watery, beech fungus (Benick, 1952).

Derodontus maculatus (Melsheimer)

(Fig. 10)

Cryptophagus maculatus Melsheimer, 1844:115. Type locality: Pennsylvania. Type? Female, LeConte Collection [MCZ], examined.

Individuals of this species are very similar to those of *D. esotericus* in head structure, general form of the pronotum, and elytral maculation. As a result, the two broadly sympatric forms have been mixed in most collections. The prominent and posteriorly curved tooth on each side of the pronotum will easily distinguish *D. maculatus*, as will the genitalic characters given in the key.

Distribution. Eastern North America from Michigan and southern Canada, south to the Carolinas and west to Oklahoma and Kansas.

Biology. Adults have been collected in numbers on *Pleurotus ostreatus* and *Pleurotus sapidus*. Larvae and adults were taken on *Pleurotus* sp. in Kentucky. Böving and Craighead (1931) recorded the larvae from a "slimy fungus below bark of dying tulip tree". Shepard (1976) has collected larvae and adults in Oklahoma and Maryland from *Pleurotus* and from unidentified rotting fungus. He has described the feeding of larvae and death feigning in the adult, and has discussed the distribution and cold adaptation of the species.

Derodontus raffrayi Grouvelle

Derodontus raffrayi Grouvelle, 1916:296. Type locality: Mt. Marsciano, Abruzzi, Italy.

This species has not been examined, but according to Grouvelle's figure, the shape of the pronotum closely resembles that of *D. unidentatus*.

Derodontus trisignatus (Mannerheim)
(Fig. 11)

Corticaria trisignata Mannerheim, 1852:361. Type locality: Sitka Island [Baranof Island], Alaska.

This species resembles *D. unidentatus* in general form, head structure, and elytral maculation, but may be distinguished by the lack of posteriorly curved teeth at the apical pronotal angles and by the structure of the median lobe (Fig. 36), which is obtusely angulate, and not acute, at the apex.

Distribution. Western coast of North America from southern Alaska, through the western parts of British Columbia, Washington, and Oregon, to Marin Co., California.

Biology. Adults have been collected on *Hericium coralloides*, *Inonotus dryophilus*, *Phaeolus schweinitzii*, and *Pholiota squarrosa-adiposa* (Hatch, 1962).

Derodontus unidentatus Lawrence, **new species**
(Fig. 12)

This species differs from *D. maculatus* and *D. esotericus* in the much narrower lateral pronotal margins, more elongate and heavily maculate elytra, and head with a complete transverse ridge, distinct boss, and smooth frontal area. It may be distinguished from *D. trisignatus* by the presence of prominent, posteriorly curved teeth at the anterior pronotal angles, flatter elytral intervals and apically acute median lobe.

Description. Length 2.0-3.0 mm. Color of head and pronotum yellowish brown to dark reddish brown; elytra yellow, each with large, dark brown to black macula extending from anterior fourth of lateral edge, mesally and posteriorly, usually touching the suture at posterior two-fifths and extending along center of disc to posterior fifth. Head (Fig. 2) with transverse, flat, distinct, median boss, wider than length of an ocellus, bordered posteriorly by deep trough, median ridge fairly broad and complete; anterior bridges broadly meeting; frontal area relatively flat and smooth. Pronotum about 0.85 X as long as wide at middle, sides sub-parallel and barely explanate, each with a single, prominent, posteriorly curved tooth anteriorly and 3 or 4 very small teeth along posterior third. Elytra about 1.8 X as long as greatest combined width and 3.9 X as long as pronotum; elytral intervals relatively flat, becoming slightly raised and forming weak carinae at anterior ends of 3rd and 5th. Sternite 9 of male (Fig. 25) with distinct pit near apex; parameres about equal in length to basal piece, each with distinct mesal notch at apical fourth; median lobe (Fig. 37) 1.1 X as long as basal piece, acute at apex.

Types. Holotype male, Bucks Lake, Plumas Co., CALIFORNIA, Oct. 23, 1960, Lot 702 J. F. Lawrence, ex *Ischnoderma resinosum* [MCZ 32635]. Paratypes: CALIFORNIA: 1, Blodgett Forest, 8 mi. E Georgetown, El Dorado Co., Oct. 25, 1966 (C. O. Dudley) [CIS]; 15, Bucks Lake, same data as holotype [CAS, JFL, MCZ]; 12, 7 mi. NE Bucks Lake, Plumas Co., Nov. 6, 1960, Lot 708 J. F. Lawrence, ex *Ischnoderma resinosum* on *Pseudotsuga Menziesii* [FMNH, JFL, MCZ, USNM]; 1, Canyon Dam, Plumas Co., Lot 713 J. F. Lawrence, ex *Fomitopsis pinicola* on *Pinus* sp. [MCZ]; 12, same locality and date, Lot 714 J. F. Lawrence, ex *Ischnoderma resinosum* on *Pinus* sp. [JFL, MCZ]; 2, same locality and date, Lot 718 J. F. Lawrence, ex *Bondarzewia berkeleyi* [MCZ]; 2, Donner, Sierra Nevada (Schaeffer Collection) [FMNH]; 2, Donner, Summit of Sierra Nevada Mts., Oct. 15, 1894 (L.E.R.) [MCZ];

3, Summit of Sierras, Oct. 15, 1894 (Roland Hayward) [MCZ]; 2, Sierra Nevada [AMNH]; 21, 1 mi. N Ice House, El Dorado Co., Oct. 12, 1970, fungus (F. Andrews) [CDA]; 2, no specific locality (Chas. Palm) [AMNH]; OREGON: 6, above Algoma, 5700', Klamath Co., Oct., 1965, toadstool fungus (J. Shuh) [JS]; 5, Little Yamsey Mt., 5700', Klamath Co., Oct. 24, 1965, coral fungus (J. Shuh) [JS].

Distribution. Known only from the central and northern parts of the Sierra Nevada range, California, and from south-central Oregon.

Biology. Adults have been collected on *Bondarzewia berkeleyi*, *Fomitopsis pinicola*, and *Ischnoderma resinosum*.

Laricobius Rosenhauer

Laricobius Rosenhauer, 1846:5. Type species, by monotypy, *L. erichsoni* Rosenhauer.

Species of *Laricobius* are easily distinguished from other Derodontidae by the vestiture of long, erect hairs, the lobed tarsi, open procoxal cavities, and elytra with 10 rows of punctures and a scutellary striole.

Distribution. Central and eastern Europe, the Caucasus, northern Siberia, northern North America.

Biology. Larvae and adults predaceous on members of the family Adelgidae (Homoptera). See pp. 387 and 388.

Key to North American Species of *Laricobius* (Adults)

1. Pronotum shorter and broader, PL/PW less than 0.68; head and scutellum much darker in color than pronotum or elytra; elytral puncture rows separated by more than 1 puncture diameter; Pacific Northwest..... *L. laticollis* Fall
- 1'. Pronotum more elongate, PL/PW more than 0.68; pronotum and at least portions of elytra as dark as head and scutellum; elytral puncture rows usually separated by 1 puncture diameter or less 2
- 2(1'). Elytra more than 3.4 X as long as pronotum, uniformly brownish or black in color; posterior edge of pronotum wider than anterior edge; Pacific Northwest *L. nigrinus* Fender
- 2'. Elytra less than 3.4 X as long as pronotum, reddish with suture and sides black; anterior edge of pronotum wider than posterior edge 3
- 3(2'). Elytral punctation coarser, number of punctures in 3rd row about 25; aedeagus with parameres narrowly rounded at apices, median lobe shorter and broader, about 1.5 X as long as basal piece; usually associated with *Adelges piceae*.....
..... *L. erichsoni* Rosenhauer
- 3'. Elytral punctation finer, number of punctures in 3rd row about 30; aedeagus with parameres obliquely truncate at apices, median lobe about 1.7 X as long as basal piece; usually associated with *Pineus strobi* *L. rubidus* LeConte

Laricobius caucasicus Rost

Laricobius caucasicus Rost, 1893:341. Type locality: western Caucasus.

This species has not been examined, but according to Reitter's key (1894) to Palaearctic *Laricobius*, it is most similar to *L. laticollis* in elytral punctation and general coloration.

Laricobius erichsoni Rosenhauer

Laricobius erichsoni Rosenhauer, 1846:7. Type locality: Tyrol, Austria.

This species is similar to *L. rubidus* from which it differs by the coarser elytral punctation and the aedeagal structure (see Brown, 1944).

Distribution. In Europe, the species occurs from the Italian Alps north to southern Denmark, west to the Pyrenees and east into the Carpathians. In North America, it has been introduced into Nova Scotia, New Brunswick, Newfoundland, Washington, and Oregon, where it has apparently become established (Clark and Brown, 1958; Hatch, 1962).

Biology. According to Franz (1958), the preferred host of *L. erichsoni* in Europe is *Adelges piceae* (Ratzeburg). See pp. 387 and 388.

Laricobius laticollis Fall

Laricobius laticollis, Fall, 1916:14. Type locality: Seattle, Washington.

Holotype, Fall Collection [MCZ 24493], examined.

This species is easily distinguished by the short and broad pronotum, fine puncture rows on the elytra, and yellowish or reddish color of pronotum and elytra, which contrasts with the much darker head and scutellum.

Distribution. Extreme northern coastal California through Oregon and Washington to southern British Columbia and northern Idaho (Hatch, 1962).

Biology. This species has been taken on at least two occasions from Douglas fir (*Pseudotsuga Menziesii*) but it has not been associated with any particular prey species.

Laricobius nigrinus Fender

Laricobius nigrinus Fender, 1945:152. Type locality: Bear Springs, Wapinitia cut-off, Oregon. Holotype, Fender Collection; paratypes examined [MCZ].

This species is characterized by the uniform black or brownish coloration, elongate form, shape and relatively small size of the pronotum. The relatively fine pronotal megapunctures, densely packed elytral punctures (within rows), and truncate parameres on the aedeagus are all similar to the eastern *L. rubidus*, which differs in having a larger pronotum with the anterior edge wider than the posterior one, and somewhat broader, bicolored elytra. The most similar Palaearctic species is *L. sahlbergi* Reitter from Siberia (Reitter, 1894).

Distribution. Oregon, western Washington, British Columbia, and northern Idaho (Hatch, 1962).

Laricobius rubidus LeConte

Laricobius rubidus LeConte, 1861:198; 1866:99. Type locality: near Washington, D.C. Holotype, LeConte Collection [MCZ 32369], examined.

This species is superficially similar to *L. erichsoni* but differs from the

latter in having finer elytral and pronotal punctation, somewhat more yellowish pubescence, and a larger aedeagus with truncate parameres and a longer median lobe. *Laricobius laticollis* has a shorter and broader pronotum, *L. nigrinus* has relatively longer elytra, and both differ in color and aedeagal structure. The species was synonymized with *L. erichsoni* by LeConte and Horn (1883), but Brown (1944) noted that the American species was specifically distinct and illustrated the genitalic differences.

Distribution. Northeastern North America from the District of Columbia north to New Brunswick and west to Michigan.

Biology. A predator of *Pineus strobi* (Hartig) on the trunks of the eastern white pine (*Pinus strobus*); uncommonly associated with *Adelges*. See pp. 387 and 388.

Laricobius sahlbergi Reitter

Laricobius sahlbergi Reitter, 1883:42. Type locality: Fatjanowsk, Arctic Siberia.

Nothoderodontus Crowson

Nothoderodontus Crowson, 1959:82. Type species, by original designation, *N. gourlayi* Crowson.

The three species in this genus are easily distinguished from other Derodontidae by the vestiture of recumbent hairs, lack of a scutellary striole, and 11-striate elytra with a deep pit at the base of stria 9, 10, and 11. The deep pits on the meso- and metathorax are similar to those in *Laricobius*, and the structure of the procoxal cavity is unique in that the trochantin is concealed by the coxal cowling. The head canals and bridges in *Nothoderodontus* are superficially similar to those in *Derodontus*, but a detailed study reveals substantial differences between the two, which have been discussed in an earlier section (p. 379). Major features of the *Nothoderodontus* head include a deep and narrow transverse canal joining the antennal insertions and two lateral canals joining a transverse canal posteriorly and crossed by two cuticular bridges; these are most evident in the illustration of *N. chilensis* (Fig. 3). Unlike those of *Derodontus*, the bridges are not closely connected to the ocelli. In *N. gourlayi* (Fig. 4) the anterior of the two bridges on each side has become broadly connected and apparently fused, so that there appears to be a single large bridge extending over a deep cavity.

Distribution. Chile, New Zealand, and southeastern Australia. The Australian record is based on a single individual of a new species taken in *Nothofagus* litter at Cement Creek, near Warburton, Victoria. The species is definitely in the *N. gourlayi* group, but it will not be described until more material is available. Another New Zealand species, represented by a single individual, has also been seen in the D.S.I.R. collection at Auckland. It is likely that the genus is more widely distributed in Chile, and it probably occurs in Tasmania as well.

Biology. The New Zealand species has been collected on and under bark chips encrusted with "fumagine" or sooty mold (Ascomycetes: Capnodiaceae). The Chilean species may have similar habits. See p. 387.

Key to Species of Nothoderodontus (Adults)

1. Pronotum more than 0.7 X as long as wide, sides expanded at middle but with very narrowly explanate edges (Fig. 13); pronotal hypomera without deep pits; antennal segments 3-6 less than 1.4 X as long as wide; head (Fig. 4) with a broad, transverse impression joining two deep, anterolateral cavities, each of which is crossed by a cuticular bridge; anterior end of metasternum with two short, longitudinal carinae just behind intercoxal process; New Zealand *N. gourlayi* Crowson
- 1'. Pronotum less than 0.7 X as long as wide, sides more broadly explanate (Fig. 14); pronotal hypomera each with a deep pit near base of postcoxal process; antennal segments 3-6 more than 1.6 X as long as wide; head (Fig. 3) with a narrower transverse canal joined to two lateral ones, and with two cuticular bridges on each side; metasternum without anterior carinae; Chile 2
- 2(1'). Lateral edges of pronotum each with 8 to 10 distinct teeth; pubescence sparser, the decumbent hairs more widely spaced, so that the shining cuticular surface is evident; mesosternum with median carina; basal piece of aedeagus (Fig. 32) without carina; median lobe (Fig. 33) with shorter basal struts and rounded apex *N. dentatus* Lawrence, n. sp.
- 2'. Lateral edges of pronotum with very small teeth, sometimes obscured by hairs; pubescence denser, the decumbent hairs covering most of the surface, creating a dull appearance at lower magnifications; mesosternum not carinate (Fig. 15); basal piece of aedeagus carinate at base; median lobe with longer basal struts and angulate apex *N. chilensis* Lawrence, n. sp.

Nothoderodontus chilensis Lawrence, **new species**
(Fig. 14)

This species is distinguished from *N. dentatus* by the denser dorsal pubescence, weakly dentate lateral pronotal edges, flat mesosternum, lack of a median suture on tergite 9, and longer basal struts on the median lobe. *N. gourlayi* has a more elongate pronotum with narrower sides, anterior carinae on the metasternum, a simpler head structure, and no hypomeral pits, in addition to the distinctive genitalia discussed under that species.

Description. Length 1.8-2.0 mm. Color uniformly reddish brown; upper surface clothed with dense decumbent, pale yellow hairs, creating a dull appearance. Head (Fig. 3) with a strongly curved transverse canal, joined on each side to an oblique, longitudinal canal which extends to the antennal insertion; posterior bridges broadly meeting, anterior ones narrowly so; eyes conspicuously setose, the setae easily visible at 60 X magnification. Antennal segments 3-6 elongate, at least 2 X as long as wide. Pronotum 0.6 X as long as broad at middle, sides strongly rounded and explanate, the edges weakly dentate, the 8 to 10 small teeth often obscured by laterally projecting hairs; disc with 3 very weak impressions. Elytra about 1.5 X as long as greatest combined width and 3.4 X as long as pronotum, each with a transverse impression at anterior third involving intervals 2 through 4; elytral intervals relatively flat and densely covered with decumbent, pale yellow hairs. Pronotal hypomera each with a deep pit at base of postcoxal process; mesosternum flat; meta-

sternum without anterior, longitudinal carinae. Sternite 9 broadly rounded at apex; tergite 9 without median suture. Parameres subacute at apices, 0.8 X as long as basal piece, which is carinate at base. Median lobe 1.5 X as long as basal piece, with longer basal struts (0.4 X total length) and an angulate apex.

Types. Holotype, male, 32 km. N Quellon, Chiloe Is., CHILE, Feb. 6, 1968 (L. & C. W. O'Brien) [MCZ 32366]. Paratypes: 4, same data as holotype [CAS, JFL].

Biology. See p. 387.

Nothoderodontus dentatus Lawrence, **new species**

This species is similar to *N. chilensis* but is distinguished by the sparser dorsal pubescence, strongly dentate lateral pronotal edges, carinate mesosternum, median suture on tergite 9, and shorter basal struts on the median lobe. *N. gourlayi* has similar pubescence, but it differs with respect to several characters given in the previous diagnosis and in the key.

Description. Length 2.0 mm. Color uniformly dark reddish brown; upper surface clothed with moderately sparse, decumbent yellowish hairs, so that the shiny surface beneath is apparent. Head with a weakly curved transverse canal; posterior bridges narrowly meeting, anterior ones barely so; eyes not conspicuously setose, the setae barely visible at 60 X magnification. Antennal segments 3-6 elongate, at least 1.7 X as long as wide. Pronotum about 0.64 X as long as broad at middle; sides strongly rounded and explanate, the edges strongly dentate, with 8 to 10 conspicuous teeth; disc with 3 moderately strong impressions. Elytra about 1.54 X as long as greatest combined width and 3.2 X as long as pronotum, each with a transverse impression at anterior third involving intervals 2 through 5; elytral intervals slightly convex, covered with decumbent yellow hairs, which are more sparsely distributed than those of *N. chilensis*. Pronotal hypomera each with a deep pit at base of post-coxal process; mesosternum with median, longitudinal carina; metasternum without anterior, longitudinal carinae. Sternite 9 broadly rounded at apex; tergite 9 with median suture. Parameres (Fig. 32) subacute at apices, 0.8 X as long as basal piece, which is not carinate at base. Median lobe (Fig. 33) 1.5 X as long as basal piece, with shorter basal struts (0.3 X total length), and a rounded apex.

Types. Holotype, female, Piruquina, Chiloe Is., CHILE, Feb. 25, 1973, No. 45 (T. Cekalovic-K.) [MCZ 32367]. Paratype: 1 male (on slide), same data as holotype [JFL].

Nothoderodontus gourlayi Crowson
(Fig. 13)

Nothoderodontus gourlayi Crowson, 1959:83. Type locality: Arthur's Pass, Canterbury, South Island, NEW ZEALAND.

This species is easily distinguished from the Chilean members of the genus by the head structure, pronotal shape, shorter antennae, metasternal carinae, and lack of hypomeral pits.

The total length of the holotype is 2 mm, according to Crowson, but specimens examined in this study are less than 1.6 mm in length as seen from above with the head declined. The structure of the head appears much simpler than in the Chilean forms, but this has been shown earlier (p. 379) to represent a derivative condition. The antennae in this species are relatively short, segments 3 through 8 being not or only slightly longer than broad, with the first two club segments distinctly transverse. The pronotum in *N. gourlayi* is about 0.8 X as long as broad, with 3 relatively deep impressions and deep pits on each side. The lateral pronotal edges are very slightly dentate, with the teeth obscured by hairs, as in *N. chilensis*. The

elytra each have several slight impressions, and the pubescence is relatively sparse as in *N. dentatus*. The ventral part of the prothorax lacks hypomerical pits, the mesosternum lacks a median carina, and the metasternum bears two longitudinal carinae at the anterior end, one on each side of the base of the intercoxal process. The 9th abdominal segment (Fig. 31) is unique in that the tergite is reduced to a narrow band mesally and lacks a median suture; the sternite is narrowly rounded at apex. The aedeagus is also unique in that the parameres (Fig. 29) are short, broad, and notched apically, while the median lobe (Fig. 30) has fused basal struts.

Distribution. Known from Arthur's Pass, Canterbury, and several localities in Nelson, South Island, New Zealand.

Biology. Collected under chips of *Nothofagus* bark encrusted with sooty mold. See p. 387.

ACKNOWLEDGMENTS

We thank the following individuals and institutions for lending or donating material to us (Abbreviations used in text placed in square brackets): American Museum of Natural History, New York, N.Y. (L. Herman) [AMNH]; California Academy of Sciences, San Francisco, Calif. (D. Kavanaugh) [CAS]; California Department of Agriculture, Sacramento, Calif. (F. Andrews) [CDA]; California Insect Survey, University of California, Berkeley, Calif. (J. Doyen, J. Chemsak) [CIS]; Canadian National Collection, Entomology Research Institute, Ottawa, Canada (E. Becker) [CNC]; Canadian Forest Service, New Brunswick, Canada (D. Eidt); T. Cekalovic-K., Concepcion, Chile; Field Museum of Natural History, Chicago, Ill. (H. Dybas) [FMNH]; G. Kennen, Stony Brook, N.Y.; Museum of Comparative Zoology, Harvard University, Cambridge, Mass. [MCZ]; C. and L. O'Brien, Tallahassee, Fla.; G. Peters, Corvallis, Ore.; J. Schuh, Klamath Falls, Ore. [JS]; K. Stephan, Red Oak, Okla.; U. S. National Museum and U. S. Department of Agriculture, Washington, D. C. (D. Anderson, T. Erwin, J. Kingsolver) [USNM]. Information on distribution and habits of *Derodontus* was provided by W. Shepard and W. Tyson, and J. C. Watt provided data concerning *Nothoderodontus gourlayi*. Mark Deyrup allowed us to use unpublished data on *Peltastica tuberculata*. The illustration in Fig. 17 was executed by S. Poulakis, and the scanning electron micrographs were taken by E. Seling. Thanks are also given to N. Hinnebusch and D. McShane for typing, M. Pearce and M. Thayer for proofreading, A. Coleman and P. Chandoha for photographic work, A. Newton for advice during portions of the study, D. R. Norris for critically reading the manuscript, and to the Museum of Comparative Zoology and the Commonwealth Scientific and Industrial Research Organization for providing various facilities. This study was made possible with the aid of National Science Foundation grants BMS 7502606 and BMS 7412494.

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